Sociality and Cooperative Maternal Care in Domestic Cats

A Dissertation submitted to the University of Cambridge
for the Degree of Doctor of Philosophy

by

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The social structures of two groups of domestic cats, leading semi-feral lives in a large outdoor enclosure, were studied. The affiliative nature of interactions and relationships within these groups was examined in the context of possible reproductive costs and benefits, particularly with respect to the occurrence of cooperative rearing of kittens.

Two forms of analysis were used to describe the social organisation of the study groups, focussing first on spatial relationships, and then on specific types of social interaction. These data were described on different structural levels, including trends across the entire colony (e.g. between the two groups and over different age and sex classes), among the various dyads, and among the individual cats making up the groups. Female behaviour patterns appeared more involved with the reinforcement of amicable relationships with other females. Most male interactions were attributable to mating-type activities or aggression. Juveniles tended to interact with one another and with more familiar adult females, as did kittens.

The reproductive state of females was used to divide the data into seasons. Both spatial and behavioural relationships were found to have a cyclic structure over the year, indicating some stability to the relationships, with consistent changes from season to season. Affiliative relationships, particularly those between cooperating females, could be predicted in advance of the birth of litters, and seemed to be reinforced throughout the year.

Once the social patterns had been delineated, different aspects of female reproduction were considered. One of the main factors was communal litter-rearing, which has been previously noted but never before described in detail for free-ranging cats. Communal litters occupied twice as many nest sites as Solitary litters, and typically left the nest about a week earlier. An estimate of reproductive success was used, and from this measure, there was some indication that kittens reared in cooperative litters (communal litters plus those with one mother and helpers) had better chances of survival. Therefore, kitten survival might be one possible benefit of cooperation.

From the investigation of sociality and differences in maternal care, the main conclusion was that, where resources allow the formation of cat groups, sociality could give rise to affiliative relationships, which in turn could act as the foundation for cooperative care of kittens. Cooperation itself might be perpetuated through enhanced survival of kittens raised by more than one care-giver.

"There are cats and cats."

Denis Diderot (1713-1784)

"Cats and monkeys, monkeys and cats - all human life is there."

Henry James, *The Madonna of the Future*

"The cat is the only animal that accepts the comforts but rejects the bondage of domesticity."

Georges Louis Leclerc de Buffon (1707-1788)

"I have studied many philosophers and many cats. The wisdom of cats is infinitely superior."

Hippolyte Taine (1828-1893)

"When I play with my cat, who knows whether she is not amusing herself with me more than I with her."

Michel de Montaigne, *Essays II xii*

A UN GATO

No son más silenciosos los espejos
ni más furtiva el alba aventurera;
eres, bajo la luna, esa pantera
que nos es dado divisar de lejos.
Por obra indescifrable de un decreto
divino, te buscamos vanamente;
más remoto que el Ganges y el poniente,
tuya es la soledad, tuyo el secreto.
Tu lomo condesciende a la morosa
caricia de mi mano. Has admitido,
desde esa eternidad que ya es olvido,
el amor de la mano recelosa.
En otro tiempo estás. Eres el dueño
de un ámbito cerrado como un sueño.

TO A CAT

Mirrors are not more wrapt in silences
nor the arriving dawn more secretive;
you, in the moonlight, are that panther figure
which we can only spy at from a distance.
By the mysterious functioning of some
divine decree, we seek you out in vain;
remoter than the Ganges or the sunset,
yours is the solitude, yours is the secret.
Your back allows the tentative caress
my hand extends. And you have condescended,
since that forever, now oblivion,
to take love from a flattering human hand.
You live in other time, lord of your realm -
a world as closed and separate as dream.

Jorge Luis Borges

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years at Cambridge. My mother, Melinda, has always supported and encouraged me, through every situation and every endeavour. Her belief in my abilities, her unfailing love and her sensible honest guidance have never flagged, and all my successes are hers. I would not have come this far without her.

There remains only one person for me to thank, and these words are not enough. He has remained patient and understanding, even through the writing-up, and he has proof-read and double-checked everything, at the cost of his own work. My heart-felt thanks and eternal gratitude go to Douglas Scott, who has enriched my life and my work, and without whom I would be bereft.

I declare that this dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration, nor any material previously written by another person, except where due reference is made in the text. This dissertation includes no material which has been submitted, or is currently being submitted, for a degree, diploma or other qualifications at any other university. The text does not exceed 80,000 words.

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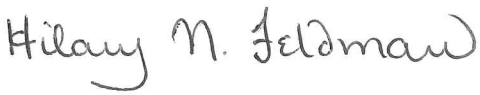

Contents

Two adult females, Pansy (left) and Katrina (centre), resting in contact, with a third female, Poppy (right) grooming herself (note raised leg). (see Section 2.3.2)

Two adult females, Wanda (left) and Molly (right), resting in contact. A third female, Jenny, is grooming herself in the background. (see Sections 2.3.2 and 4.6)

Chapter 1

Introduction

1.1. GENERAL INTRODUCTION

Free-living cats can be divided into three groups, based on their dependence on people: 'housecats', 'farm cats' and 'feral cats' (Passanisi & Macdonald 1990). More than one million feral cats live in Britain (Rees 1981; Passanisi & Macdonald 1990), and they are particularly concentrated in areas of human habitation. These cats show flexible behaviour and an ability to adapt to changing circumstances, and provide an opportune subject for the investigation of how ecological factors affect individual differences, as well as the structure and growth of populations. The past two decades have seen a plethora of studies on aspects of sociality and predation effects in various cat populations. One factor which remains particularly poorly understood is the phenomenon of cooperation in cat groups, and how such behaviour is linked to social structures and individual relationships. The following chapter presents an overview of the domestic cat, with reference to the characteristics it shares with other felid species, and also within the context of carnivore societies.

The first section of this chapter (Section 1.2) summarises much of what is known about the domestic cat and the way in which it lives (in the context of sociality); it is divided into three subdivisions. The first segment is a synthesis of the current information about the domestic cat, starting with a review of the taxonomic placement of the cat and its evolutionary origins (Section 1.2.1.1). Then the definition of "social" animals is examined, along with a presentation of the literature dealing with cats as both solitary and group-living carnivores (Section 1.2.1.2). The third area concerns territoriality and the diverse measures of home ranges in free-living cats (Section 1.2.1.3); and the last part of the first half (Section 1.2.1.4) is a critique and comparison of the wildcat with the domestic cat. In the second segment of Section 1.2, the theoretical framework for studies of social groups is presented (Section 1.2.2.1), along with the potential costs and benefits of group-living (Section 1.2.2.2). The third segment gives a brief discussion of individual differences (Section 1.2.3), and suggests that such differences may affect groups and their organisation.

In the second section of the chapter (Section 1.3), a variety of reproductive aspects are reviewed. The first consideration is the mating system of felids (Section 1.3.1), followed by some details about reproduction in small cats (Section 1.3.2). Then the theory concerning cooperation is merged with some observations of cooperation in cats (Section 1.3.3), followed by a discussion of infanticide and its potential relevance in cat studies (Section 1.3.4). The last part examines some details about the development, in the sense of ontogeny, of domestic kittens (Section 1.3.5).

The third section of the chapter (Section 1.4) summarises the component chapters of the thesis and indicates many of the questions guiding this study. This chapter reviews the information available on domestic cats and their sociality, in order to establish the background for the present study: an examination of the ways in which social behaviour and female reproduction interact.

1.2. SOCIAL ORGANISATION

1.2.1. THE DOMESTIC CAT

1.2.1.1. *Evolutionary Origins and Taxonomy*

The domestic cat, *Felis silvestris catus*, has a rather unknown evolutionary past, and the frequent changes in its classification reflect the taxonomic uncertainty. It is now included as a subspecies of the European wildcat, *Felis silvestris*, along with the putative primary ancestor, the African wildcat, *Felis silvestris libyca* (Van Vechten 1952; Kolb 1977; Liberg 1981; Nowak & Paradiso 1983; McFarland 1987); much of the debate is fuelled by the lack of morphological variation between the skeletons of the domestic cat and its possible wild ancestors (Wright & Walters 1980; Serpell 1988). All cats are classified under the Family Felidae (Haltenorth & Diller 1980; Wozencraft 1989), which includes both the so-called big cats (Pantherinae and Acinonychinae) and the small cats (Felinae); they derived from a common viverrid-like ancestor in the Miocene period, approximately ten million years ago (Stains 1975; Martin 1989; Wayne et al. 1989), and have the greatest range in size of modern carnivores, yet the least morphological variation (Wozencraft 1989).

Analysis by albumin immunological distance suggests that the small cats, all of the genus *Felis*, are monophyletic and diverged over several million years (Wayne et al. 1989); all the species examined have an identical karyotype (2n=38) which differs from that of other felids (Robinson 1979; Wayne et al. 1989; Wozencraft 1989). Further genetic studies support this proposition with the same retroviruses being present in the DNA of all individual cats (Wayne et al. 1989). Retroviruses are viruses containing RNA; multiple copies of each type (the domestic cat has at least two families, FeLV and RD-114) are found in the normal DNA of all individuals. Protein sequences homologous with these particular endogenous retroviruses support the monophyletic evolution proposed for the *Felis* genus and suggest ancestral links with further felid groups (Wayne et al. 1989). Fertile hybrids have been produced from domestic cats with the European wildcat (Kirk 1935), African wildcat, jungle cat (*F. chaus*) and steppe cat (*F. caudata*); other, probably

sterile, crosses have been achieved between the domestic cat and the bobcat (*Lynx rufus*), black-footed cat (*F. nigripes*), leopard cat (*F. bengalensis*), and tiger cat (*F. tigrina*). Hybrids of unknown fertility were produced from the European and African wildcats; the creation of so many viable combinations illustrates the karyotype similarities among most small cats as well as other felids (Robinson 1979).

Felids are well-adapted for their carnivorous lifestyle and specialise in concealment and sit-and-wait predation strategies. Most of the small cats have long tails and retractile claws, but other features vary somewhat (Haltenorth & Diller 1980). The African wildcat resembles the domestic cat but is generally larger and tends to have a lighter pelage coloration; it is found throughout most of Africa, Asia Minor, the Near East and India, reared kittens are tameable (Haltenorth & Diller 1980), and it has a generally more compliant nature than other wildcats (Wright & Walters 1980; Serpell 1988). The swamp or jungle cat, *Felis chaus*, is another potential ancestral species to the domestic cat (Wright & Walters 1980; Tabor 1983) and overlaps with much of the range of the African wildcat, incorporating nine subspecies; it differs from the African wildcat only in the possession of a shorter tail and less distinct patterns on the body (Haltenorth & Diller 1980) and in skull structure (Wright & Walters 1980). The European wildcat, *Felis silvestris*, is first known from the lower mid-Pleistocene, or about one million years ago (Wayne et al. 1989); it is approximately one third larger than the domestic cat, with long dense fur, longer legs, a broader head and shorter, blunter tail than *F. s. catus* (Kirk 1935; Nowak & Paradiso 1983). Although it may have played a role, through hybridisation, in the genesis of the domestic cat (Hamilton 1896; Kirk 1935; Van Vechten 1952; Wright & Walters 1980), the European wildcat remains relatively intractable when reared; modern hybrids with domestic cats bear little behavioural resemblance to the domestic cat in terms of tameness (Serpell 1988).

The domestication of the cat probably occurred in North Africa around 2000-3000 B.C. (Vesey-FitzGerald 1969; Todd 1977; Robinson 1980; McFarland 1987), although the reasons and the process are debatable (see Serpell 1988). In comparison with other domestic animals, the cat was tamed more recently and with less complete effects; a domestic cat reverts easily to a wild lifestyle in the absence of an owner and, while kittens can be tamed up to seven or eight weeks, subsequent generations are free-living and often unapproachable (Hall & Pelton 1979; Remfry 1979; Tabor 1981). The designation "feral" describes such an independent cat (Liberg 1981; Liberg & Sandell 1988), while still of the same species of the ordinary domestic cat (UFAW 1981); a feral cat can therefore be defined as a cat of the domesticated variety (e.g. species) which has since reverted to a wild state (after Tabor 1981). This is also the legal definition as used in England (e.g. a feral cat is "one that has reverted from a domestic to a wild animal"; Neville & Remfry 1984). This includes individuals which have themselves been pets or their free-living descendants.

1.2.1.2. *Social Versus Solitary Lifestyles*

Very few mammalian species, whether solitary or group-living, fail to interact with other conspecifics (Ewer 1973; Kerby & Macdonald 1988); in this sense, "solitary" is not the converse of "social", but instead implies certain things about the possible levels and types of interaction. Sandell (1989, p.164) defines "solitary" in the following manner: "A carnivore is solitary if it never, except when mating, cooperates with conspecifics; that is, if two or more animals of any given species cooperate to rear young, forage, achieve matings, or defend against predators, the species is classified as cooperative". Because of the high incidence of intra-specific variation in carnivore sociality, Sandell goes on to specify that the existence of any cooperative populations defines the whole species as cooperative, even in the light of a widespread lack of such sociability. Other authors have used different criteria for the distinction of solitary species, particularly of felids, in that the females of such species are intolerant of conspecifics except during mating with males and litter-rearing, females maintain exclusive ranges and lack persistent matrilineal associations, and males overlap female ranges (Packer 1986).

The basic felid social system has been proposed for many of the larger cat species, and some of the smaller populations as well (Sunquist & Sunquist 1989). It involves female dependence on resource distribution, with the potential for overlap in female ranges regulated by temporal separation of use by different individuals; females rear young alone and hunt singly. Males maintain larger exclusive ranges which incorporate the areas of several females. The large size of prey and generally open nature of the habitats of big cats may be the major determinants of the spatial distribution. By the terms of the definition proffered by both Packer (1986) and Sandell (1989), these felid species would be "solitary"; a similar system was first advanced for feral cats, and indeed for their wild counterparts. However, it is becoming increasingly evident that many felids previously thought to be solitary in this sense are more socially interactive (e.g. cheetah: Eaton 1970, 1979; leopard: Ewer 1973; margay: Petersen 1979; tiger: Ewer 1973), albeit not necessarily cooperative in the terminology of Sandell (1989). "Solitary" is not necessarily the converse of "group-living", and also does not carry the implication of interacting only for mating purposes, in that a "solitary" species can display diverse forms of social interaction. Thus "solitary" can be seen as distinct in many ways from the broader category involving group-living or not, and from the idea of being "asocial".

Group-living is less prevalent in the carnivores than among mammals generally (Gittleman 1989). Groups can form in a variety of contexts, including the use of a common home range, during feeding, foraging or breeding, but always involve more than two conspecifics joining in some mutual structure. The possible costs and benefits of

group-living are discussed at length in Section 1.2.2.2. along with various aspects of group formation and maintenance. The remainder of this section concerns the variation observed in domestic cat populations between those cats who are observed to live alone (or solitarily in the less strict sense) and those found in groups. Due to the existence of cooperative rearing in cats (Section 1.3.3), the species will herein be described as "cooperative" using the definition given by Sandell (1989) and "solitary" will be taken to indicate those cats not resident in groups, as is the common usage in most cat literature.

A number of studies have found cats, particularly feral ones, leading a solitary lifestyle (Fox 1975b; Laundré 1977; Corbett 1978; Leyhausen 1979; Jones & Coman 1982; Konecny 1983), althought they rely on a variety of definitions of solitary. In most of these cases, the populations were observed in an isolated location, ranging from sub-antarctic islands to the Galapagos, and were completely dependent on natural prey such as rabbits and other rodents (Jones 1977; Corbett 1978; George 1978). Solitary females were usually observed alone or in the company of their kittens and immature juvenile offspring (van Aarde 1978; Konecny 1983); even where the population was described as solitary, cats were occasionally seen in groups, although rarely comprising multiple adults. The persistence of mother-offspring relationships beyond the age of independence may be indicative of the potential for social groupings based on matrilineal kinship. Certainly, where resource limitations force animals into isolated lifestyles, the maintenance of any social and spatial bonds outside of the dependent period (of kittens) either suggests a high level of social potential and/or fierce intraspecific competition for resource-linked ranges. In the latter case, the sharing of a range with offspring might enhance a female's reproductive success more than forcing them to disperse (Packer 1986). Other evolutionary benefits might then accrue, and adult groups could then be maintained under a variety of resource distributions.

Female cats have been commonly seen living in social groups of 2-7 adults plus offspring (van Aarde 1978; Dards 1979, 1981; Liberg 1981; Neville 1984), with an observed maximum of 20 or more females in some cases (Izawa et al. 1982); in the case of Dards (1978), 75% of all females in the study site were living in stable groups. Several authors have proposed an intermediate system, with partial pair-bonds (Kleiman & Eisenberg 1973; Scott 1976; Corbett 1979), but most studies have rejected that as a major possibility for cat social groups. Natoli (1985) observed females living with their offspring for at least two consecutive generations (also in Fagen 1978), and this may demonstrate the establishment of female matrilines thought to underlie the structure of social groups (Kerby & Macdonald 1988). As has been proposed for primates (Berman 1983b), lineages may show differences in social cohesion as regulated by affiliative interactions.

Within a group, little antagonism was observed (Macdonald & Apps 1978; Izawa et al. 1982) while amicable relationships were identified (Macdonald & Apps 1978;

Panaman 1981; Kerby 1987). Group-living cats were in frequent social and physical contact (Kerby & Macdonald 1988). It was rarely possible to discern a dominance hierarchy (Panaman 1981; Tabor 1981; Izawa et al. 1982), although some authors have distinguished them among group females (Baron et al. 1957; Cole & Shafer 1966; Laundré 1977). De Boer (1977) suggests that increasing familiarity may reduce dominance relationships, indicating that some of the differences seen by researchers may result from the diversity of populations studied and the stability of these groups.

Males tend to be somewhat more nomadic, and mainly visit female groups for mating access (Liberg 1980; Turner & Mertens 1986). Some males do live in multi-female, and occasionally multi-male, groups while most others are resident in a particular area (Liberg 1981; Tabor 1983) that overlaps with female groups. Often a single male range may encompass several female groups (Dards 1979). It is possible that the basic unit of a female and kittens may be a more efficient way to exploit patchily-distributed food sources (e.g. provisioned food or discrete colonies of prey), while the dispersal and larger ranges of males may allow the use of transient food sources (e.g. seasonal abundance of various prey species) and prevent inbreeding (Dards 1979). The dual strategies of resident versus nomadic males also appears to occur in other cat species, such as puma and bobcats (Liberg & Sandell 1988).

Domestication has been suggested as the source of cat sociality; whatever the cause, group structures exist in both "domestic" and feral populations (Fitzgerald & Karl 1986). This proposal will be explored further (see Section 1.2.1.4). Several features overlap in the consideration of group-living, and these are approached separately in the following sections; related aspects include territoriality and home ranges (Section 1.2.1.3), the mechanisms of group structure (Section 1.2.2.1), and the various advantages and disadvantages of groups that determine their viability in any given population (Section 1.2.2.2).

1.2.1.3. *Home Ranges and Territoriality*

The concept of home ranges versus territories should be explored before summarising the details known for cats. A home range is an area in which an individual lives; if this region is defended actively by the resident animal to the exclusion of others, then it is more completely defined as a territory (Fitzgerald & Karl 1986). Different factors can affect the size of a range, including the general size and resource requirements of a species, the sex, age or reproductive state of an individual (Wright & Walters 1980; McFarland 1987; Liberg & Sandell 1988). The spatial pattern of any population reflects individual attempts to maximise survival and reproductive potential (Sandell 1989), and resource distribution, in turn, determines the constraints at work. Cats have been found

living in densities ranging from one individual to 2000 cats per square kilometre; this variation was thoroughly reviewed in Liberg and Sandell (1988).

In cats, home ranges usually consist of a food source, resting areas and connecting paths (Izawa et al. 1982) which are used fairly consistently. Groups often centre around a central food source, and the home ranges of these feeding congregations do not tend to overlap, but remain predominantly exclusive to group members (Liberg 1980; Izawa et al. 1982). Active defence of resting sites (Izawa et al. 1982) or ranges in general (Dards 1979; Liberg 1980) has not been seen, precluding the idea of territories in cats, but the stability of feeding group membership suggests some interdiction of intruders. Females tend to use a core area more than the rest of the range, while males are more consistent in range use (Leyhausen & Wolff 1959; Dards 1979; Panaman 1981). In one study, males were seen to use the perimeters more and showed more variation in range size (Haspel & Calhoon 1989).

The use of common pathways has been seen in several feral cat populations (Fox 1975b; Izawa et al. 1982), and a degree of range overlap seems tolerated by males and females alike (Fox 1975b; Macdonald & Apps 1978; Corbett 1979; Natoli 1985; Fitzgerald & Karl 1986; Kerby & Macdonald 1988). Turner and Mertens (1986) reported an average overlap of 14% between all females, with 55% between members of the same group and only 4% between residents of different groups; males were more overlapping, with a total average of 19%, distributed such that group members shared 57% and inter-group males 14% of their range areas. Males would appear to be more tolerant of other males than females are of other females, particularly between different groups (Dards 1979). In fact, female groups are essentially exclusive of one another (Liberg 1980, 1981; Turner & Mertens 1986).

Relatively few studies have provided thorough data on the spatial habits of other felid species. Male bobcats have ranges approximately twice as large as those of females (Litvaitis & Harrison 1989), and these remain fairly stable throughout an individual's tenancy; females maintain fairly exclusive ranges, while male ranges tend to overlap with those of other males as well as females (Bailey 1974). Prey density would appear to be a key factor in the range sizes of many wild species (Liberg & Sandell 1988); food sources are the major determinant of female range size and the degree of overlap, while males are governed by both food and access to females (Liberg & Sandell 1988).

Female cat ranges may be influenced by the distribution of suitable sheltered sites in the habitat, such that young kittens can be kept concealed and safe (Dards 1981; Natoli 1985), as well as by the availability of sufficient food for the support of lactation costs (Dards 1979; Liberg 1980). Male distribution, on the other hand, may be more affected by the availability of females and the presence of other conspecifics (Liberg 1980), or just by the size of the area available (Dards 1979). In one study, however, the size of

home ranges appeared to be due to differences in body weight and not to the availability of females, as indicated by the constancy of range size in spring (mating season) and autumn; the availability of garbage (potential food) and empty buildings (shelter), seasons, and provisioning had no apparent influence on range size (Haspel & Calhoon 1989). Urban cats appear to have smaller ranges than rural individuals, perhaps due to the increased food availability (Oppenheimer 1980) or to the limitations of high cat density in urban areas; in fact, in urban regions, food may well be surplus and not limiting, and therefore play little role in the determination of range size for cat inhabitants, who are limited by other factors (Todd 1977; Haspel & Calhoon 1989).

Feral cats appear to have larger home ranges than neighbouring house cats (Liberg 1981, 1983b, 1984a). Increases in cat density are associated with decreases in range size (Dards 1979; Turner & Mertens 1986), particularly for females (Liberg & Sandell 1988). Rank may also influence range size, such that more dominant animals tend to have larger regions (Turner & Mertens 1986). Although a ratio of ten to one has been reported for male to female range sizes in cats (Dards 1981; Tabor 1983), other studies do not find such a large division between the sexes (Turner & Mertens 1986; Liberg & Sandell 1988; Haspel & Calhoon 1989).

Feral cats were predominantly nocturnal in their activities in some studies (Izawa et al. 1982; Haspel & Calhoon 1989), although other studies and other circumstances found them more diurnal (Panaman 1981; Fitzgerald & Karl 1986), especially in the winter (Dards 1979; Izawa et al. 1982; Liberg 1984b), or occasionally crepuscular (Corbett 1979). Bobcats tend to be diurnally active (Litvaitis & Harrison 1989), with no apparent seasonal effect on daily patterns. Lions, leopards, cheetahs and servals are also primarily diurnal, while other felids are seen in the daytime only when the weather is cooler and more cloudy (Haltenorth & Diller 1980).

The presence of juveniles does not appear to affect the spatial distribution of adult cats; in addition, juveniles show a preference for their natal area (Natoli 1985) until the age of dispersal. The dispersal of young animals may be one of the more important ways in which the density of animals remains relatively constant (Natoli 1985), and involves the movement of individuals away from the natal area. Male dispersal is particularly common in mammalian species, especially primates (Colvin 1983) and carnivores (Bekoff 1989). Where females remain in their natal groups, the age at first conception is usually larger than the period of male residence for the purposes of breeding (e.g. the siring males tend to have moved to other groups by the time their daughters reach sexual maturity); in this way, females may passively avoid inbreeding with closely related males (Clutton-Brock 1989). However, if females do not show a mild breeding suppression, but stay in the natal range, other means of minimising inbreeding include the

dispersal of breeding males and active inbreeding avoidance by either the males or females (Liberg 1984b, Clutton-Brock 1989).

The potential costs of inbreeding include the expression of deleterious genes, the loss of any advantages of heterozygosity, and the intensification of inter-sibling competition (Bateson 1983; Partridge 1983). In lions, inbreeding has been demonstrated to have a detrimental effect on reproduction, through a decrement in sperm viability and a reduction in testosterone production (Wildt et al. 1987). Ways of avoiding unnecessary inbreeding should therefore be adaptive to all individuals involved in reproduction. However, outbreeding also has its costs, and these include the suppression or loss of environmentally adaptive genes, the loss of co-adaptive allelic combinations, the loss of highly related offspring (in polygynous species), the costs of dispersal and emigration, the loss of environmentally-adaptive skills (or mis-matching with new populations), and the increased likelihood of exposure to new pathogens from a mate (Bateson 1983; Partridge 1983).

Obviously, the costs of both inbreeding and outbreeding should be balanced, and the optimal situation will depend on environmental conditions as well as genetic factors. Within a single species, huge differences in breeding constraints may be found such that some populations are very inbred, showing that inbreeding cannot be uniformly damaging (Bateson 1983); in other species, inbreeding may have detrimental consequences (Wildt et al. 1987). Domestic cats appear to be able to tolerate a degree of inbreeding without deleterious results (see Section 1.3.1), although the tendency for male dispersal may decrease the likelihood of extreme inbreeding.

If groups are founded by female alliances, then male behaviour is secondary to group formation (Moss & Poole 1983; Wrangham 1983b). Males tend to be the dispersers in cat populations (Liberg 1980), thereby minimising their own chances of inbreeding, while females remain in the natal group (Dards 1979; Wrangham 1983b). Emigration in primates can occur at a range of ages after independence is reached (Colvin 1983), while in cats, most males leave the natal group around the time that they attain sexual maturity. It is likely that aggression from the adult male is a key mechanism fuelling dispersal (Dards 1979); younger animals are first peripheralised and then gradually leave in the face of agonistic rejection from the adult male (Colvin 1983). Competition between male peers may also contribute to the phenomenon of dispersal (Colvin 1983), as may differences in social bonds with peers and adults (Bekoff 1977).

1.2.1.4. *A Comparison of Feral Cats and Wildcats*

Few studies have actually examined the European wildcat in sufficient detail for the purposes of comparison with other cat species; in fact, given that intra-specific

variation is so widespread, it is a bit surprising that the results of these sparse data are so universally relied upon. Unfortunately, the species is extremely scarce in most of Europe, and the logistics of carrying out such a study prohibit extensive further research. The European wildcat, *Felis silvestris*, lives in a variety of habitats, including forested, open and rocky country (Lydekker 1896; Jenkins 1961; Corbett 1979; Nowak & Paradiso 1983); it is mainly nocturnal and crepuscular (De Leuw in Kolb 1977; Corbett 1979) and generally avoids areas of human population. This is in contrast to the feral cat which, as discussed previously, is generally found near human centres due to the availability of provisioned food.

The major study of the wildcat was done by Corbett (1979) in Scotland; most of the observations were taken by telemetry, and wildcats were actually seen only nine times over the course of the study, indicating the difficulties of gathering behavioural data on these animals. The author gained the impression that wildcats were usually solitary but that ranges might show some overlap. The support for categorising the wildcat as solitary and territorial lay in the observation of variations in range size, the exclusivity of some home ranges (especially for resident adults), the failure of young animals to settle areas already occupied, and the territorial aspects of scent-marking; however, no overt defence of ranges was seen (Corbett 1979). Many of these characters have also been seen in certain feral cat populations (Corbett 1979). Ragni (1978) saw some social interaction and minor group associations in wildcats living in Italy, while De Leuw (in Kolb 1977) noted some pair-bonding.

Much of the variation in domestic cat populations, from solitary to group-living individuals, has been attributed to differences in food availability, in that densely clumped food sources allow the formation of larger groups. In the same light, the wildcats studied fed primarily on lagomorphs (Jenkins 1961; Corbett 1979), which showed regular cyclic patterns in population size, and might represent a relatively homogeneous and low density food source. Perhaps in other areas, were wildcats able to occupy them without interference from humans, more concentrated prey would promote more overlap and the possibility of group formation, much as has been seen in feral domestic cats.

Reproductively, wildcats are quite similar to domestic cats, and development follows the same general pattern (Section 1.2.2). Some people associated with wildcats report the occurrence of communal care of litters, albeit in more confined situations (T. Moore, pers. comm.; Leyhausen 1988); it is unlikely that short-term captivity could bring about radical changes in sociality and the potential of cooperation were they not present in the species already, and this might suggest more affinities between the social behaviour of wildcats and domestic cats. Were this the case, then the commonly voiced opinion that domestication is the source of most domestic cat sociality and cooperation would be proven incorrect; domestication may itself have been facilitated by the flexible

sociality of some small cat species, such as is seen in the African wildcat (Smithers 1968; Serpell 1988; Gittleman 1989) and probably the European wildcat (Kolb 1977; Ragni 1978; Wright & Walters 1980; Leyhausen 1988).

1.2.2. GROUP STRUCTURE

1.2.2.1. *The Underlying Mechanisms*

"Social organisation is the behavioural organisation (type, temporal, and spatial) of the society's members. Analysis of social organisation is the most complex endeavour an ethologist can undertake, because it necessitates the integrative analysis of social behaviour both within and between group members. This includes the development of social behaviour in the individual (socialisation) and the interaction of group members over time (social phases)" (Lehner 1979, p.221). In order to examine social organisation, it is necessary to focus on certain aspects of social behaviour at various levels, including interactions, relationships and overall structure (Hinde & Stevenson-Hinde 1976; Hinde 1983). Social interactions are encounters in which both participants influence the other's behaviour, while relationships involve a series of such social interactions over some time (McFarland 1987); in turn, a social structure is determined by its constituent relationships and influences them as well (Hinde & Stevenson-Hinde 1976; Hinde 1983). In other words, "social organisation is the set of all interactions among types of individuals" in a group (Gordon 1987; McFarland 1987).

The distances between individuals (or "proximity") can help to indicate the nature of existing relationships (Fox 1975b; Taber & Thomas 1982; Hinde 1983; Sekulic 1983; Kerby & Macdonald 1988; Goldizen 1989); behavioural data are also necessary to describe fully any social structure (Hinde & Stevenson-Hinde 1976; Hinde 1983). Non-random proximity relationships are a basic indicator of an active social structure (Rowell & Olson 1983; Kerby & Macdonald 1988), while the details of behavioural interactions serve to demonstrate the nature and specific organisation of the group. Relationships can change with time and context, reflecting changing pressures on the individuals, and differences may be present between reproductive and non-reproductive seasons or varying periods of food availability (Harper 1981; Hinde 1983; Wrangham & Rubenstein 1986). As a result, the same pair of individuals can behave amicably in one situation and agonistically in another (Wright & Walters 1980). Some relationships may also be density-dependent and fluctuate with demographic changes (Armitage 1977). The structure of any society is thus dependent upon the ecological conditions surrounding it, and the individual characteristics of the constituent members (Jarman 1974; Crook et al. 1976).

"Social behaviour is any action directed by an individual towards a member of its own species. It includes both competitive behaviour, such as fighting, threat and submission, and cooperative interactions such as parental care and mating" (Poole 1985, p.1). Differences can exist between age and sex classes, animals of varying status and degrees of relatedness, as well as with environmental features (Barash 1973; Nowicki & Armitage 1979; Hinde 1983; Penzhorn 1984). Food availability, resource dispersion and seasonal variation are known to affect the rates and nature of social interactions within a single group of primates (Lee 1983b); usually, as food availability increases, social interactions become more frequent and prolonged (Lee 1983b; Rood 1986). Many species have groups organised along matrilineal kinship, and appear to prefer association with related animals; although the ability for kin-recognition would facilitate such choices, most species probably use simple correlates of kinship (Hinde 1983), such as degrees of familiarity (e.g. visual, olfactory or auditory cues). Where a population has a high level of infant mortality, the probability is that group members are not extremely close kin as a result of limited survival (Morse 1980; Seyfarth 1983), and social bonds and familiarity maintain the group.

Certain types of behaviour, while having immediate functions, may also have a role in the maintenance of social bonds. One such activity is grooming in primates (Seyfarth 1983), which allows both the removal of ectoparasites and the long-term affiliative contact between any two individuals. In cats, behaviour such as rubbing and allogrooming are thought to have some part in the structure and upkeep of dyadic and group relationships (Tabor 1981; Kerby 1987; Macdonald et al. 1987). Some form of cooperation seems necessary to the formation of groups, in an evolutionary context (Wrangham 1983a). The cooperative rearing of offspring may provide some enhancement of the potential for social bonds, as has been suggested for cat populations (Fagen 1978; Schär 1985), in that kittens are early to form relationships with group members other than their mothers.

1.2.2.2. *Costs and Benefits*

In order to maintain a specific adaptive social behaviour in the species, it must have a heritable framework on which natural selection can act (Hinde 1983), and the benefits must outweigh the costs of such activity. The following discussion does not take into account those traits which are either non-adaptive or passively carried along with other genetic characters. This section explores the potential advantages and disadvantages accruing to individuals living in groups, and sets up the basis for understanding the balancing of variables underlying the formation of groups and their maintenance through social behaviour.

Possible benefits to group-living include increased defence against predators, efficient exploitation of food resources, the potential for social learning, and advantages in competition for limited resources, such as mates and territories (Eaton 1979; Macdonald 1983; Wrangham & Rubenstein 1986; McFarland 1987). Where prey is abundant, relatively large or easy to capture, and in clumped patches, groups may be a more efficient way of defending and exploiting the resource (Corbett 1979; Wrangham 1983b); small, dispersed prey, and those that are difficult to obtain, may preclude benefits to groups, and animals in such conditions may remain solitary due to strong food competition (Corbett 1979; von Schantz 1984). Other possible advantages, in some habitats, involve cooperative rearing of young (Macdonald & Apps 1978; Corbett 1979; Macdonald & Moehlman 1982; Wrangham 1983b; Kerby & Macdonald 1988), huddling for warmth (van Aarde 1978; Gittleman 1989), and the potential for enhanced social and physical development in the presence of non-parental care-givers (Wrangham 1983b).

Possible detrimental aspects of groups include the subordination of some individuals (possibly resulting in decreased reproductive success), increased conspicuousness to predators, increased transmission of disease or ectoparasites (Eaton 1979; Gittleman 1989), and more intense intraspecific competition (Gittleman 1989; Janus 1989). The particular set of ecological features affects the structure of each population, allowing a wide range of social manifestations within the same species, as well as inter-specifically (Macdonald 1979; Macdonald 1981).

The advantages of group-living may be quite different for the males and females of a species or population (Wrangham 1983b; Wrangham & Rubenstein 1986). Social behaviour is used, ultimately, to enhance an individual's chances of successful reproduction. In this sense, males pursue access to females for mating (i.e. mating is a key factor), while females act to balance the pressures of resources, predation and disease to optimise their own and offspring survival (i.e. maintained health for themselves and their young is a major factor). As a result of the disparity in selective pressures, either males and/or females may form groups without necessitating a similar structure in their mating counterparts. Multi-male, multi-female groups arise only where the various advantages of such a formation is of net benefit to individuals of both sexes, or where constraints prevent other types of group organisation. Lions are known to form such groups (Bertram 1976), or prides, however multi-male, multi-female groups are not widespread among felid species.

The group-living of two felid species can be explained by using a combination of factors: the lion may benefit from predator defence, increased food access, female coalitions for the rearing of young and male coalitions for access to females (Bertram 1976; Packer & Pusey 1982); the cheetah occasionally benefits from group use of patchy prey sources and male coalitions for mating opportunities (Eaton 1979; Caro &

Collins 1987). In other circumstances, the cost of grouping may be too high for individuals in cheetah populations, due to the potential for increased intra-specific aggression or the limitations of a smaller prey species (Corbett 1979). Thus, with variation in habitat and specific ecological factors, different populations of the same species can show enormous contrasts in structure, from lone individuals to complex groups. The costs and benefits of group formation fluctuate not only with environmental changes, but also with individual animals (Hinde 1983; Macdonald 1984), and give rise to the diversity of communities seen in many species, particularly carnivores.

Many of the influences thought to affect home range sizes and territories in cats, as briefly mentioned earlier (Section 1.2.1.3), also determine group formation and structure as another aspect of the spatial distribution of a population. It has been suggested that the social system of small cats may be indicative of the organisation of early carnivore ancestors (Kleiman & Eisenberg 1973); the use of cryptic coloration and lying in wait for animal prey would seem to promote hunting by lone individuals. Cats are little troubled by other predators when adult, and so it is relatively safe to have a system wherein individuals travel and hunt singly (Kleiman & Eisenberg 1973). If prey densities are high and food is plentiful, sharing unlimited resources is more practicable than trying to defend the resource. Once a group has been established, it can be used to defend the mutual source and exclude intruders (Wrangham & Rubenstein 1986). The availability, dispersion and quality of potential food sources undoubtedly dictate the possibilities for the foundation of groups (Macdonald & Apps 1978; Liberg 1981; Macdonald 1984; Neville & Remfry 1984; Schär 1985; Carr & Macdonald 1986), as does the nature of shelters (Fagen 1978; Kerby 1987). With the behavioural potential for stable relationships, a clumped and dependable resource distribution allows group formation, and further benefits of grouping can then be evolved (Corbett 1978).

1.2.3. INDIVIDUAL VARIATION

Domestic cats show great individual differences in behaviour (Kerby 1987; Mendl & Harcourt 1988). The set of specific activities, their frequencies and intensities, can help to define overall categories to describe individuals; these, in turn, may help to summarise the spectrum of behavioural styles (Mendl & Harcourt 1988). Individual variation has been seen in other species, including wild mice (Hurst 1987), yellow-bellied marmots (Armitage 1977) and many primate species (Clark & Ehlinger 1987), and may have a variety of effects. For example, animals of different status may co-exist with minimal competition through diverging individual characters (e.g. dominant versus subordinate in primates); changes in the surrounding conditions (e.g. food, shelter,

weather, habitat) may also confer advantages to different individuals, depending on their ability to exploit the resources and other aspects of behavioural adaptability (Bateson & Turner 1988).

Differences in behaviour may arise for several reasons: in an unpredictable environment, heterogeneity may confer some advantage on those animals with flexible behaviour; individuals may vary in behaviour due to disparate demands dependant on age, sex or size class, so that at any instant sampled animals may display a given set of characteristics; or, individual differences may be relatively unimportant in terms of reproductive success and selection, so they are carried along with other features and not selected against (Slater 1981; Clark & Ehlinger 1987). Flexibility, or the alteration of behaviour (or ecology through behaviour) to increase an individual's chances of contributing offspring or other kin to subsequent generations, depends on the specifics of the situation in which an individual is living; in contrast, developmental plasticity is the potential of a given genotype to leave more than one phenotype or to follow more than one developmental course, depending upon the early environment in ontogeny, and this gives rise to the concept of alternative strategies (Caro & Bateson 1986; Clark & Ehlinger 1987; Martin & Bateson 1988). Not all behavioural flexibility must be defined in the strictest sense, and variation can arise from short-term changes as well as from fluctuations over individual lifetimes and multiple generations.

Several of the aspects which come under the broad term "individual variation" can potentially have a formulating and modifying influence on social organisation (Armitage 1977; Slater 1981), just as the social structure may affect the individuals (Hinde 1983). A cat which spends a marked amount of time alone or away from others can be described as "solitary", with no specification of the causes of such isolation; conversely, an individual which is commonly near others and interacting with them might be called "sociable" or "central". An "amicable" cat could be one with predominantly non-aggressive encounters, as opposed to an "agonistic" cat, which shows almost no pro-social or contact behaviour. Other categories have been considered by other authors (Feaver et al. 1986; Turner et al. 1986; Karsh & Turner 1988; Mendl & Harcourt 1988; Mertens & Schär 1988), but these have often been in the context of human relationships with pets, and had little apparent bearing on the understanding of free-living and feral cats. However, the concept of differences in behavioural character may affect the establishment and structure of any group with a given set of members (Berman 1983b; Martin & Kraemer 1987). Solitary cats may not maintain social bonds and, in such cases, the group configuration may appear less cohesive; "sociable" individuals may constantly reinforce amicable relationships (Armitage 1977) and so stimulate the construction of a close-knit community with features perpetuating the group, such as cooperation.

The potential for the inheritance of qualities which affect behaviour and "personality", e.g. the set of behavioural characteristics, (Hinde 1983; Turner et al. 1986; Kerby 1987; Mendl & Harcourt 1988) may allow the formation of a diversity of populations, each patterned by the subset of attributes from the founding members. This genetic component is certainly complemented by environmental factors, which can affect the development of sociality (Mendl 1986) and other characters. Even within the same population, intra-group variation can engender different strategies, or distinct behaviour types, which can co-exist and are maintained by natural selection (Martin & Kraemer 1987); in such cases, individual differences can obscure trends, and conclusions about the group may reflect little about the actual characteristics of the group or of the members. Statistics can be adversely affected, in that central trends (e.g. means and medians) obtained by conventional descriptive statistics may be meaningless, and true effects harder to detect, because of the intra-group variability (Slater 1981; Martin & Kraemer 1987).

Other behavioural aspects which can show individual variation include specific activities and their form, frequency or duration. Parental care can vary enormously (Clark & Ehlinger 1987), as will be discussed in later sections (Sections 1.3.2 & 1.3.3); in fact, any behaviour can show differences, and these will be explored in subsequent chapters (see Chapters 3 & 4).

1.3. REPRODUCTION

1.3.1. MATING SYSTEMS IN FELIDS

The essential procedures involved in mating are more or less the same across felid species (Liberg 1981), although different species demonstrate separate tactics. Most felids are polygamous, with multiple partners (usually successively), and polygyny (one male mates with several females) is common (Liberg 1983; Natoli & De Vito 1988). The domestic cat is typically polygynous, although individual females are known to have multiple male partners. The remainder of this section will discuss mating in the domestic cat.

The details of the behaviour involved in the physical process of mating have been thoroughly described by Michael (1961), and will not be discussed here. Although some studies of the domestic cat report inter-male competition for access to oestrus females (Scott 1976; Liberg 1981; Tabor 1989), others argue that males show little aggression in the context of mating opportunities (Natoli 1990). Differences in access gave rise to the definition system in Liberg (1981), such that males fell into separate classifications: Breeders were a select few individuals with priority for mating opportunities in female

groups, usually only one to a group; Challengers were males two to three years old, who courted females as peripheral participants, occasionally clashed with Breeders, and many of whom became Breeders themselves when three to four years old; Novices were young adult males who avoided inter-male conflict and had a minimum of mating opportunities; and Outcasts were dispersed Novices who remained slightly outside the area but still attempted to court females occasionally. Males younger than 12-14 months were Juveniles and played no role in the mating system; they were seldom the recipients of adult male aggression. Courting males came in two modes, those who were Central (usually the local Breeder) and Peripheral individuals (mainly Challengers, Novices and Outcasts). Other studies have failed to distinguish any one Central male, with his attendant monopoly on most mating, or even consistently Peripheral individuals (Natoli & De Vito 1988; Natoli 1990).

Up to five males were seen courting a single female (Liberg 1981, 1983), although the number varied with time as cats came and went; in more dense populations, as many as sixteen males have been observed courting a female (Natoli & De Vito 1988). Inter-male aggression in this context was of a mild nature, and rarely escalated to full fights (Liberg 1981). Older and heavier animals had more successful mating attempts (Liberg 1981), and these tended to be Breeder and sometimes Challenger individuals. Female cats appear to exert no active mate choice and have been seen mating with multiple males in the same oestrus period, even the same day (Fox 1975b; Liberg & Sandell 1988; Natoli & De Vito 1988). Possible explanations for the absence of female choosiness include the potential benefits of a heterogeneous litter if mating with different males can give rise to a multiple-sire litter (Natoli & De Vito 1988), decreased male aggression to young with the uncertainty of paternity (Bertram 1976; Natoli & De Vito 1988), and the prospect of sperm competition and the maximisation of paternal quality (Alcock 1984; Natoli & De Vito 1988).

1.3.2. PARENTAL CARE IN FELIDS

The domestic cat is an induced ovulator (Kleiman & Eisenberg 1973; Dards 1979; Poole 1985). Adult males possess penile spines (Ewer 1973) which can vary in size depending on their hormonal state (Tabor 1989); these spines or papillae are thought to stimulate follicular rupture from the ovaries during mating (Tabor 1983, 1989). Adult male feral cats have 130-190 barbs on the penis, mainly concentrated in a barb zone around the sides, although this varies among individuals; the spines vary from paired structures in sockets to perpendicular and wedge-shaped, and there are larger spines at the base formed from the fusion of up to 4 separate barbs (Tabor 1989). Several copulations are necessary before the female becomes fully fertile, and stimulation must occur in the right part of the

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cycle. Ovulation takes place 25-27 hours after copulation, and a fertilised blastula is generally implanted around two weeks later (Scott 1976). A female cat in very poor health (e.g. one which is starving) may not ovulate at all (Hammond 1981).

Before continuing, it is probably appropriate to define several terms used in the ensuing discussion. The first of these is the concept of "investment". It is generally taken to mean any efforts made by a parent that enhance the offspring's chances of survival while having a detrimental effect on the parent's ability to put effort into future reproduction (Trivers 1972). This can include the energetic costs of gamete formation, fetal maintenance and lactation, among other things (Keverne 1985; McFarland 1987). Strictly speaking, as the entire reproductive history of most animals is unknown, "investment" should read as "effort" for most studies. In this thesis, "investment" will be taken to mean the theoretical input by a parent (with concomitant costs), and is included where the original author used the specific term.

The second term is "fitness", which is defined as "a measure of the relative ability of the animal to leave viable offspring" (McFarland 1987, p.189). It is a value which is specific to a given environment (Dunbar 1982; Trivers 1985) and the set of morphological, physiological and behavioural features of an individual (McFarland 1987); "fitness" is an ultimate term, and refers to the evolutionary adaptiveness (e.g. through natural selection) of individual characteristics in delivering offspring into future generations (Dunbar 1982; McFarland 1987). The proximate way that "fitness" manifests itself is through "reproductive success", or the actual number of offspring that an individual manages to rear to reproductive age (and through subsequent generations, although the measure of this, in terms of the number of generations which should be included, is much debated and almost impossible to follow through all the descendants; Dunbar 1982). In this thesis, "fitness" will be limited to references where that particular term was used, and "reproductive success" describes any measures of offspring survival in this and similar studies. "Inclusive fitness" is treated somewhat separately, however, and is discussed in Section 1.3.3.

As in most carnivore species (Ewer 1973; Poole 1985), young are born in a semi-altricial state, and are deaf (Ewer 1973; Deag et al. 1988), blind (Wright & Walters 1980; Martin & Bateson 1988), immobile (Deag et al. 1988), and unable to thermoregulate properly (Blaza & Loveridge 1984; Deag et al. 1988). Altricial mammals have a higher maternal reproductive input for any given gestation period and maternal weight than do precocial mammals; they also have a relatively short gestation period (Martin & MacLarnon 1985; May & Rubenstein 1985). A mother must rear her kittens and completely provide for them until they are both nutritionally and behaviourally independent; this usually requires the acquisition of sufficient prey to fulfil all the nutritional needs of both herself

and the developing offspring. Lactation is an extremely costly activity (Deag et al. 1987, 1988), and requires a huge energetic commitment from mothers (especially relative to the smaller costs of gestation and fetal growth) in terms of producing milk sufficiently rich in energy and nutrients to maintain the early rapid growth of offspring (Gittleman & Thompson 1988; Clutton-Brock et al. 1989; Oftedal & Gittleman 1989). With such a weighty responsibility, altricial species are less prone to overlapping reproductive cycles (Ewer 1973) and the potential for several dependent litters than precocial species, so although females are polyoestrus they do not have a post-partum oestrus (Kleiman & Eisenberg 1973; Dards 1979; Liberg 1983a).

Domestic cats commonly have two litters per year (Lydekker 1896; Liberg 1981; Kerby 1987), however,this number can be boosted by artificial lighting and constant rearing conditions, as in laboratories (Scott 1976; Tabor 1989). Feral cats are seen to give birth throughout the year (Dards 1979), but most births are seasonal and peak in the spring. The winter months (especially October-December) tend to find females anoestrus and little mating occurs (Tabor 1989). Increases in daylight length trigger the onset of oestrus (van Aarde 1978; Follett 1985; Tabor 1989) and rising prey abundance may be another factor causing seasonal breeding patterns (van Aarde 1978). Gestation is roughly 65 days (Scott 1976), and litters vary from one to eight kittens (Scott 1976), with a mean of four (Dards 1979; Oftedal & Gittleman 1989) to five (Deag et al. 1988). However, in feral populations, litters are typically smaller (mean=3; Dards 1979) due to harsh environmental conditions relative to the home or laboratory. Since domestic cats have eight nipples (Scott 1976; Nowak & Paradiso 1983; Deag et al. 1988), this figure should represent a practical upper limit to litter size, provided that all nipples are functional (although this is subject to some debate, as discussed in Deag et al. 1988).

The wildcat, *F. silvestris*, while usually producing one litter per year (Hamilton 1896; Moelk 1979), is occasionally seen to have two, both in captivity and in the wild, and is a strictly seasonal breeder (Kirk 1935; Kolb 1977; Corbett 1979; Tabor 1989); oestrus lasts 5-8 days, gestation lasts 63-69 days (Corbett 1979), with one to eight kittens per litter (mean ranges from 3 to 6) (Ewer 1973; Corbett 1979; Gittleman 1989). As with domestic cats, most litters are born in the spring, especially May (Kolb 1977; Corbett 1979). Wildcats become independent when they are approximately five months old (Nowak & Paradiso 1983). The putative ancestor to the domestic cat, *Felis libyca*, is reported to produce similar littersizes (mean=3), after a gestation of about 58 days (Hemmer 1979), and *libyca* kittens reach independence around 4-5 months (Gittleman 1989). The jungle cat, *Felis chaus*, another possible ancestor, gestates for 66 days. In fact, the smaller species of cats, especially those in the tropics, have been reported as seasonal breeders (Corbett 1979), prone to two litters per year, with an oestrous cycle caused by the loss of a litter, as in domestic and wildcats (Ewer 1973).

Female groups are known to develop an oestrus synchrony, the "Whitten effect", and this has been reported in lions (Ewer 1973), domestic cats (Liberg 1981; Ohkawa & Hidaka 1987), certain pinnipeds (Mead 1989) and various other species (Poole 1985).

The content of the milk produced by the domestic cat is similar to that analysed in larger cats, such as the lynx, leopard and cheetah (Ewer 1973); it is rich in fat and protein (relative to that of the cow or man), at 6.3% and 10.1% respectively for fat and protein content, and contains relatively less lactose (Ewer 1973; Blaza & Loveridge 1984). Cats have an unusually high protein requirement (Simonson 1979), probably due to their limited ability to regulate transaminases and ureacycle enzymes (Blaza & Loveridge 1984); kittens are particularly dependent upon milk to satisfy their protein needs. By mid-lactation, the gross energy content of milk is 0.9-1.7 kcal/g, which is in a similar range with the milk of the domestic dog and red fox (Oftedal & Gittleman 1989). In general, carnivore milk has moderate to high energy density for terrestrial mammals. Off-setting the high quality of cat milk, felids are reputed to have the lowest milk transfer rates of the major carnivore families (Oftedal & Gittleman 1989).

In domestic cats, the first feeding normally takes place within 1-2 hours after birth (Ewer 1961), and mothers typically spend almost all their time with the litter over the first two days (Baerends-van Roon & Baerends 1979; Deag et al. 1988). Wildcat (*F. silvestris*) kittens grow about 12 grams per day, which is similar to the measure for the sand cat, Bengal cat, fishing cat and the larger felids, as well as the domestic cat (Hemmer 1979; Oftedal & Gittleman 1989).

Female felids typically use nest sites, or dens, in which to raise their offspring (lion, leopard, cheetah, caracal, serval, sand cat, black-footed cat, kaffir cat, swamp cat: Haltenorth & Diller 1980; domestic cat: Moelk 1979 and Fitzgerald & Karl 1986; wildcat: Lydekker 1896; Corbett 1979); these are secluded locations, and remain unenhanced by the use of any nesting materials (Corbett 1979). Nests provide a crucial shelter from predation and exposure to adverse weather (Deag et al. 1988), and are particularly prevalent in species with altricial young (Poole 1985).

Young kittens can be very vulnerable when they leave the nest, with the possible dangers of straying and becoming lost (e.g. loss of warmth and nutritional sources when they are separated from both nest and mother), or attack by predators. Kittens have a tendency to huddle together, which may be adaptive behaviour, and which helps with the retention of heat (Rosenblatt 1976; Baerends-van Roon & Baerends 1979), and are also able to emit a high-pitched distress call (Deag et al. 1988; Peters & Wozencraft 1989). They rarely leave the nest until four or five weeks old, unless moved by a care-giver (Corbett 1979; Dards 1979), but are able to relocate a nearby nest even at the early age of

several days (Deag et al. 1988) using olfactory and thermal cues, along with rudimentary movements.

There is no male parental care in the domestic cat, feral cat or wildcat (Corbett 1979; Wright & Walters 1980; UFAW 1981). There may be some male parental investment, by the definition proposed in Kleiman and Malcolm (1981), which includes "any increase in a prereproductive mammal's fitness attributable to the presence or action of a male". Indirect forms of investment may include scent-marking, patrolling, vocalising and the expulsion of intruders, all regular features of a territorial male's behaviour. Direct forms of male parental investment are more focussed on the kittens, and have been observed only in captive felids, including the wildcat; these are activities such as huddling with young, retrieval of young, grooming, feeding, and active defence (Kleiman & Malcolm 1981). Free-living felids appear to direct few beneficial aspects specifically toward kittens, but kittens may profit from male territoriality (e.g. through expulsion of potentially infanticidal intruders) and may be included in a male's activities when he approaches the mother.

The form of parental care may vary between individuals, as can the quality of the relationship between parents and their offspring (Carlisle 1982; Clark & Ehlinger 1987); in goats, younger females often leave their young for long periods of time (e.g. "leavers"), while older females forage near their offspring and remain with them for longer intervals (e.g. "stayers"). In time, "leavers" tend to become "stayers" (not vice versa), and this may be due to pressures changing from the need for high-quality food (in the smaller females) to the constraints of predation and the need to stand guard (in larger, older and healthier females). Maternal parity and rank, as well as infant sex and the presence of other individuals, can influence maternal activities and the time spent with offspring in primates (Hinde 1983; Hooley 1983; Lee 1983a; Clark & Ehlinger 1987) and red deer (Clutton-Brock & Albon 1982), among other mammals. The effects of "good", "bad", and "indifferent" care can be measured by infant mortality or the long-term social and reproductive success of offspring (Clark & Ehlinger 1987).

Domestic cats also show differences in individual maternal style, such that parity, littersize, maternal condition and other factors appear to affect the mother-kitten relationship (Gallo et al. 1980; Deag et al. 1988; Mendl 1986, 1988a & b). In the wild, still more variables may prove to influence kitten growth, survival and future success. With increases in the age of offspring, the benefits to the young of maternal care decrease, while the costs of such care increase for the parent (Trivers 1972, 1974; Hinde 1983; Taborsky 1985). Another aspect of maternal care in cats is the phenomenon of communal care and cooperation.

1.3.3. COOPERATION

Communal care has been observed in a variety of mammalian species (Spencer-Booth 1970), including at least 7 Orders (Harper 1981), amounting to approximately 15% of mammalian species (in Gittleman 1985). Several hypotheses have been put forward to try to rationalise this apparently paradoxical behaviour (in terms of natural selection), which involves seemingly unrewarding efforts on the part of non-parental, and often non-kin, individuals. Generally, communal care can be defined as a form of cooperation in which individuals other than the parents aid in the rearing of offspring (Gittleman 1985; McFarland 1987); these "helpers" have been intensively studied in many bird species (Davies 1982), but are somewhat less well-known in non-primate mammals (Swartz & Rosenblum 1981). Activities can be directly performed towards young, for example nursing, guarding, grooming, retrieving and feeding, or indirectly affecting young, for example defence of territory or resources (Kleiman & Malcolm 1981).

Communal species show a wide assortment of forms; these include the pooling of offspring by female groups, breeding pairs with non-breeding helpers (usually older offspring) and helpers in multi-female, multi-male groups (Bertram 1976; Gubernick 1981; Lee 1983a). Communal species often display delayed sexual maturity in females and a long period of development (Wilkinson & Baker 1988).

In elephants, allomothering is common, usually performed by kin (especially nulliparous, adolescent females), and rarely involves suckling (Lee 1987). In prairie dogs, an estimated 68% of juveniles received milk from allomothers, perhaps resulting from an inability to discriminate young in pooled litters (Hoogland et al. 1989). Communal nursing is a particularly expensive form of care, as sharing milk with offspring other than one's own might reduce the allomother's reproductive success in limiting conditions (Wilkinson & Baker 1988).

Explanations for cooperation refer to the concepts of effects on inclusive fitness (through kin selection) , reciprocal altruism (for unrelated group members) (Trivers 1971; Bertram 1976; Macdonald 1981; Maynard Smith 1982), and mutualism, whereby each collaborator benefits at the time (Macdonald & Moehlman 1982; Rubenstein 1982; Wrangham 1982). Other possibilities are that cooperation is a form of altruism which is compelled by social pressure, or that it is simply nonadaptive (Bertram 1982), although these offer little evolutionary explanation. Inclusive fitness relates to the conditions for the "initial increase and ultimate fixation of a gene for altruism" (O'Donald 1982) and is defined by O'Donald (1982) as "an individual's own fitness plus [its] effect on [its] relatives' fitness weighted by [its] degree of relation to them" (see Grafen 1982). It necessitates that only closely related individuals cooperate, and relies on the following assumptions: that inclusive fitness is enhanced by behaving cooperatively (Gubernick

1981); and that helpers are themselves unable to breed for some reason (Morse 1980; Moehlman 1986). As yet, there are no firm data that show a definite benefit through increases in helper fitness for mammals (Bekoff 1981).

Reciprocal altruism occurs between related and unrelated individuals, and involves a temporary reduction in the altruist's reproductive productivity; theoretically, non-kin should only be helped when the species has long life expectancy, low dispersal rates and stable groups, individual recognition, and dominance relationships which allow reciprocity (Bertram 1976; Harper 1981). Later benefits do not have to take the same form, and can accrue through social bonds, increased survival, higher status and other factors; however, it is difficult to equilibrate different aspects, and reciprocity is generally taken to mean actions in which "repayment" is in the same coin as the initial act (Bertram 1982). Senescent females have less likelihood of reproducing, and might aid others without threat to their own interests (Harper 1981) while reinforcing social relationships. In the dwarf mongoose, unrelated immigrants are seen to help the dominant group female, along with subordinate adults and yearlings (Rood 1986); in this way, they may be able integrate themselves into the group in order to gain the benefits of living together, and perhaps eventually breed themselves. Both these cases may be examples of mutualism, with different types of benefits accruing to the individuals involved.

In domestic cats, communal effort has been seen in diverse forms, including cooperative suckling (Fagen 1978; Macdonald & Apps 1978; Macdonald 1981; Kerby 1987), allogrooming (Fagen 1978; Macdonald 1983; Kerby 1987), guarding (Liberg 1981; Macdonald 1981), and the provision of food (Macdonald & Apps 1978). Other social behaviour, such as playing with kittens and resting in contact, is shown in both related and unrelated animals (Fagen 1978; Kerby 1987). The synchronisation of female breeding facilitates communal suckling (Gittleman 1985), although that may not be its primary function. Actual aid during parturition (e.g. cleaning and chewing the umbilical cord) has also been observed in cats (Macdonald et al. 1987).

It is widely proposed that cat society is based upon matrilineal kinship groups (Liberg 1984b; Kerby 1987; Kerby & Macdonald 1988), such that, in free-living populations, females remain with their natal group (creating a long-term association between mothers and their female descendants), while males tend to disperse at maturity. Gubernick (1981) suggests that matrilines may favour selection for communal care of offspring; the implication is that inclusive fitness would be enhanced for all members of the group, through both their own offspring and through those of closely related females. Therefore, cooperative rearing should be more common among members of a matriline than among unrelated females. This seems to be the case in several studies of unconfined and feral cats (Dards 1979; Kerby 1987), especially where matrilines are separated into distinct feeding groups.

If familiarity is the working basis for recognising kin (Wu et al. 1980; Hinde 1983; Ferkin 1988), then cats reared together will be treated as kin regardless of their true degree of relatedness; in this case, once females have pooled kittens, subsequent generations will associate as if part of the same kinship group (Bekoff 1981). A further feature is brought in by the spatial system. If several females are based on a site such as a farm, they may be kin or non-kin, depending on the farmer's method of obtaining cats; if the farm is somewhat isolated, it is possible that only one male might include it in his range. Therefore, all kittens born to the farm cats will be related paternally, so that, as further generations act like kin, there will be a parallel increasing level of relatedness within the group. In this way, an unrelated group of females can initiate a true matriline after several generations (and in cats, with females potentially breeding in their first year, this may take only a few years).

It is possible that communal care in cats is the result of a combination of reciprocal altruism, mutualism (in unrelated females) and kin selection (in related females), stemming from the close social ties formed in female groups (Macdonald & Moehlman 1982). The choice of communal partners may depend on past association and the tenor of the dyadic relationship, or on some phenotypic cue (Wilkinson & Baker 1988).

Much of the theory surrounding the question of communal care involves the potential costs and benefits of such behaviour; ultimately, every rationale must return to natural selection and the reasons why cooperation might arise and persist in a species. Costs and benefits can be found for separate contexts, whether measured for the parents, offspring or helpers; different participants are subject to different constraints and outcomes, and these will change over time (Trivers 1985).

Possible benefits include the following effects: improved chances of adoption if mother is injured, killed or neglectful (Harper 1981; Swartz & Rosenblum 1981; Hamilton et al. 1982); increased defence against infanticidal males or predators (Morse 1980; Harper 1981; Kerby & Macdonald 1988) through enhanced vigilance or a dilution effect (Gittleman 1985; Hoogland et al. 1989); temporary increases in status or reduced aggression (Bekoff 1981; Harper 1981); increased probability of offspring survival (Morse 1980; Harper 1981; Wrangham 1983b); communal suckling and food acquisition (Bertram 1976; Gittleman 1985); allogrooming (decreased ectoparasites); aid in thermoregulation (not in warm months)(Wilkinson & Baker 1988); and increased territorial defence or tenure (Gittleman 1985).

Potential detrimental effects include the following possibilities: attraction of predators or increased aggression (results of increased density); the mixing of offspring in pooled litters; rapid transmission of disease and ectoparasites; infanticide; premature displacement of a resident breeder; and increased competition for resources such as food, mates and breeding sites (Wrangham 1983b; Gittleman 1985; Kerby & Macdonald 1988).

Fundamentally, helping must not be overly harmful, or it would not be tolerated by mothers (unless it evolved under circumstances that no longer persist).

The distribution of resources, and any variation in their availability, can have large effects on social organisation in a species (Corbett 1979; Kerby & Macdonald 1988; see Section 1.2.2.2); where resources are more unpredictable, animals tend to have larger litters (with runts), the possibility of abandonment, infanticide and/or cannibalism, and juvenile dispersal (Lack 1948; Harper 1981). As the social organisation can vary within and between populations, depending on resources (as has been postulated to explain the variability reported for cats), the presence of alternative strategies may optimise reproduction under changing conditions (Harper 1981; Carlisle 1982; Hinde 1983).

In a recent review of littersize effects, primarily in rodents, Mendl (1988b) reports that individual differences in behaviour and development may partially be generated by natural variation in littersize. On average, communal litters, as the combination of several groups, are larger than single litters; if littersize affects individuals, then communally-reared offspring may generally differ from those raised solitarily. For example, independence may come sooner in communal nests, and these animals might be more prepared for social interactions with unfamiliar cats (and therefore fit into the group more readily).

Regardless of the possible advantages of cooperative rearing, conflict should still occur, as all females will act to maximise the returns while minimising the expenditure; individuals can be selfish and nurse only their own young (individual selection), or they can cooperate with kin (kin selection), or they can bank on the probability of future returns with non-kin (reciprocal altruism)(Wilkinson & Baker 1988).

Recognition of a female's own young is not necessary where separate nest sites define litter identity (Gubernick 1981; Hoogland et al. 1989); if common dens are used, it is possible that mothers can recognise individually their own offspring (Poole 1985). It is controversial whether cats are able to distinguish different kittens; Ohkawa and Hidaka (1987) found that, based on retrieval behaviour, some females appeared able to recognise their own offspring and others could not. One cheetah female appeared unable to distinguish between her own young and another cub (Gubernick 1981). Indiscriminate suckling takes place in some females and not in others (Ohkawa & Hidaka 1987; Kerby & Macdonald 1988). Allosuckling in communal cats is still only partially understood, and has been the focus of few studies; if results generally indicate that cats may be physiologically unable to identify their own kittens, it might be postulated that they have evolved to rear litters in separate nests, and cooperation is a new phenomenon in phylogenetic history. Or perhaps cooperation is such an old and advantageous behaviour that there is no need to distinguish one's own young within the nest. Similar arguments can be imagined for the case in which females can consistently recognise their own kittens.

The reproductive factors surrounding cooperation and communal care in free-living cats will be further investigated and discussed in Chapter 5: Maternal Behaviour.

1.3.4. INFANTICIDE

Mothers themselves may be responsible for cases of infanticide in their litters, through active killing or passive abandonment; explanations focus on the idea of cutting present losses and the maximisation of future opportunities, therefore allowing adjustment to a littersize optimal for the conditions (Harper 1981; Wickler & Seibt 1983; Gittleman 1985). Helpers have also been reported to perform infanticide, possibly for competitive reasons or as a prelude to cannibalism, in lions, spotted hyaenas and ground squirrels (Gittleman 1985).

In cats, several cases of infanticide by unrelated males have been reported (Spencer-Booth 1970; Macdonald et al. 1987); this has also been seen in mountain gorillas (Watts 1989), lions (Bertram 1976), baboons (Gomendio & Colmenares 1989), langurs (Trivers 1985; Huntingford & Turner 1987), and sea lions (Campagna et al. 1988) among other species. Infanticide by males has sometimes been taken to support the sexual selection hypothesis for its evolution, such that interbirth intervals are reduced, and females are more likely to be receptive to mating with the loss of their infant (Watts 1989). In sea lions, however, infanticide appears to be an occasional incidental outcome of pup abduction for the purposes of sexual mounting; also, in baboons, infanticide is a rare result of attacks (when infants interrupt male-female interactions), and the return to oestrus is independent of the death of infants (Gomendio & Colmenares 1989). A recent paper considering infanticide in domestic cats suggests that gestation times and inter-birth intervals in this species are sufficiently shorter that infanticide speeds the reproductive process relatively little and may bring few benefits to males (Natoli 1990). Perhaps this helps to explain the infrequency in reports of male infanticide in domestic cats.

Another, slightly different, insight is offered by the evidence that, in lions, mothers with small offspring delay returning to the pride when older cubs (more than 3 months old) are present (Macdonald & Moehlman 1982). This could correspond to the observation of spring-born kittens (e.g. 3 to 4 months old) playing roughly with neonates, drawing blood, and leading to the rapid disappearance of the newborns (this study). In other words, the possibility of multiple dependent litters in a single year allows the potential for interference between consecutive litters despite the relative independence of the older kittens. There is no indication that this is due to competition, but could be the outcome of burgeoning talents for object play and the capture of small prey.

Very few species are reported to exhibit intense communal care, involving allosuckling, and infanticide; one such example is the prairie dog (Hoogland et al. 1989),

and another is the domestic cat (Macdonald et al. 1987). In some prairie dog populations, females suckle the post-emergent (e.g. 6 week-old) pups of close kin; in these groups, lactating females often kill the young offspring of kin (pre-emergent), causing a 30% mortality rate over all litters. Behaviour ranges from females who kill young and never foster to those who foster and never kill. Hoogland, Tamarin and Levy (1989) propose two explanations; the first is related to individual recognition, such that pre-emergent litters are easily discriminated, and it is possible to nurse one's own pups and kill any others. After emergence and the pooling of litters (possibly to reduce predation costs), discrimination may be too costly a development, so infanticide stops and communal nursing becomes commonplace.

The second theory invokes food scarcity in early lactation; as cannibalism often follows infanticide, unrelated offspring may serve as an important food source while they are small and defenceless. It would be detrimental to kill all non-related pups, as this would render multilitter groups impossible for defence purposes. Both hypotheses suggest that communal care and infanticide are self-serving actions that enhance the actor's offspring at the cost of others. However, no mechanism for regulation is put forward, so that it is difficult to see how any litters survive the pre-emergence phase.

A third possible explanation, and one that could pertain to domestic cats, is that in species with well-developed communal care, females may kill the kittens of other females to maximise their own gains from cooperation (Dards 1979; R. Pierotti, pers. comm.). Infanticidal females may reduce their own efforts for unrelated kittens, while increasing the proportion of care coming to their own litter. Again, this relies on the ability to recognise one's own offspring (see Section 1.3.3) and requires a mechanism by which all females do not act this way (thus destroying all offspring each year).

The sex of infanticidal individuals is a key part of explaining how such behaviour arises and persists in any species. Both males and females have occasionally been seen in situations suggesting infanticide (and not just cannibalism of a previously dead individual) in wildcats (Conde & Schauenberg in Corbett 1979) and domestic cats (Macdonald et al. 1987; A. Garcia-Bellido, pers. comm.). For males and females, the nutritional aspect of cannibalism is a possibility; also, males may act to try to induce oestrus in females, despite evidence that this does little to speed reproductive cycling, as explained earlier. Female guarding of kittens should minimise the opportunity for such male actions. Females may commit infanticide for any of the reasons given above (in the case of unrelated kittens) or to reduce reproductive efforts in the face of unpredictable resource limitation (Harper 1981; Wickler & Seibt 1983).

1.3.5. KITTEN DEVELOPMENT

In the domestic cat, kittens weigh 85-110 grams at birth (somewhat lighter than the wildcat, at 137g)(Scott 1976; Oftedal & Gittleman 1989), they are only thinly covered in fur and the ears are partially folded; kittens' eyes do not open for 7-20 days after birth (Baerends-van Roon & Baerends 1979; Dards 1979), and solids are consumed from about 32 days (Deag et al. 1988; Oftedal & Gittleman 1989). This is similar to other small felids, such as *Felis nigripes*, whose young are a bit lighter. In *F. nigripes*, the black-footed cat, the eyes open at 6-8 days and solids are eaten around 35 days after birth (Ewer 1973); in the Bengal cat (*F. bengalensis*), the first solid food is reported at 44 days, later than many other small cats (Oftedal & Gittleman 1989). Wildcat (*F. silvestris*) kittens typically open their eyes around day 11, and walk by day 18 (Hemmer 1979).

A general developmental sequence is found in cats, as with many other vertebrate species, in that the order of developmental systems follows from tactile to olfactory to vestibular and auditory and then to the visual system (Rosenblatt 1976; Martin & Bateson 1988). A comprehensive review of kitten development, including sensory, physiological and motor features, is provided in Martin and Bateson (1988).

Weaning is the process during which the rate of parental investment falls sharply and the young move rapidly towards independence (Martin 1982; Deag et al. 1988). In domestic cats it starts at four weeks, and is completed around seven to eight weeks after birth (Dards 1979; Martin 1986; Deag et al. 1988), with a growth discontinuity around 30-32 days, corresponding to the time at which solid food starts to dominate the diet (Moelk 1979; Bateson & Young 1981; Deag et al. 1987). In the first two weeks, kittens develop responses to thermal, tactile and olfactory stimuli (Baerends-van Roon & Baerends 1979; Martin 1982); vision becomes refined by three weeks, and locomotion by four weeks (Frederickson & Frederickson 1979). Social responses, to visual and olfactory stimuli, are initially developed from about six weeks (Kolb & Nonneman 1975; Deag et al. 1988). Teeth are fully erupted by five weeks, and at this age, kittens are able to fully use solid food sources.

The timing of weaning may have some effects on some behaviour patterns, including object and social play (Bateson & Young 1981; Tan & Counsilman 1985). Play activities are a noticeably large part of the kitten's behavioural repertoire, developing from about four weeks (Barrett & Bateson 1978; Baerends-van Roon & Baerends 1979) and continuing well into the first year or longer. Several studies offer a comprehensive examination of the potential association between weaning and play (Bateson 1981; Bateson & Young 1981; Martin 1982; Martin & Bateson 1988; Bateson et al. 1990; Smith 1990) and predation behaviour (Caro 1979; Caro 1980a & b; Tan & Counsilman 1985).

1.4. AIMS OF THE STUDY

Despite an increase in the number of studies on domestic cats, several aspects have never been fully examined. Laboratory studies are unable to investigate the social relationships involved in the structure of free-living groups, while field studies have been constrained in the availability of animals for social interaction and the close appraisal of maternal reproduction. This study was designed to investigate the phenomenon of communal care in an outside colony, and to look for correlates in the social structure of the group that might help to explain this behaviour in cats.

The first part of the study involves an examination and description of the basic social structure of the two cat groups comprising the outdoor colony. This was done through observation of spatial and behavioural encounters, and was analysed on three basic levels: for individual cats; for dyadic relationships; and for the group as a whole, including different age and sex classes. The second part of this study involves an analysis of variables concerned with female reproduction and certain types of maternal behaviour. The last part of the study combines the social behaviour and reproduction findings, and uses these results in the formulation of an explanation for sociality and cooperation in cat groups.

The thesis is organised into the following sections:

Chapter 2 describes the set-up of this study, including the enclosure itself, the individual animals in the colony, and the data collection regime. All behaviour patterns are defined and the details of general data treatment are described, along with statistical methods.

Chapter 3 examines the spatial relationships of the group members, at three levels: the colony (sex and age classes), the dyad, and the individual. Spatial data are then considered for seasonal changes. Weather variations are also analysed for possible effects on spatial relationships.

Chapter 4 reviews the behavioural relationships of the group members, at the level of the colony (sex and age classes), at the dyadic level, and also for individuals. Behaviour patterns are then considered for seasonal changes. Weather variations are also analysed for possible effects on behavioural relationships.

Chapter 5 investigates the details of maternal behaviour, kitten survival and kitten development. Four dimensions are considered: inter-group differences; primiparous versus multiparous mothers; communal versus solitary care; and individual differences. Other factors such as reproductive success and the numbers and locations of nest sites are presented.

Chapter 6 synthesises the information provided in the previous three data chapters and analyses the underlying mechanisms of the sociality seen in cat groups.

Chapter 7 provides a summary of the main results and gives the general conclusions.

An adult male, Zac (right), close sniffing the anogenital region of an adult female, Molly (centre). A second adult female, Jenny, watches on. (see Sections 2.3.2 and 4.2.1)

An adult male, Zac, mounting a juvenile female, Cleo, who is four months old. A younger kitten sits nearby. Cleo later twisted free and ran away, after an unsuccessful mating attempt. (see Sections 4.2.2. and 4.4.4)

An adult female, Calico (centre), hisses at an adult male, Zac (right), who is attempting to mount her. He also attempted to mount the juvenile female, Cleo, to the left, and met with the same response from Calico (Cleo's mother). (see Sections 4.2.5 and 4.3.2)

Chapter 2

General Methods

2.1. THE STUDY SITE

2.1.1. THE ENCLOSURE

2.1.1.1. *Layout*

The enclosure covered an area of approximately 1600 square metres near the periphery of the Sub-Department of Animal Behaviour, at Madingley. It was formed by 4 high wooden walls supported by concrete pillars, with remaining walls made from metal mesh. The wooden sides were about 6 metres high, while the mesh sides were 3 metres high. Cats were unable to leave by climbing the mesh because of a complicated overhang on top of the perimeter fence; the construction was such that a cat would be required to walk upside-down along a short section before reaching a proper foothold for surmounting the fence. The overall enclosure was L-shaped, with an observation tower built into the inside corner; the observation room featured windows facing into each arm of the L, and was reached by a path along the outside of the perimeter (Figure 2.1).

The area was divided into two roughly equal sections prior to the start of the study, to allow the establishment of two adjacent populations; the dividing fence resembled the wire perimeter fences, with an overhang at the top to discourage escape. The nature of the dividing fence material meant that inter-group interactions could occur, which was a drawback to the study. However, as will be discussed later, these interactions were relatively rare, and confined to certain patterns of behaviour. Inside the fences, the habitat was both natural and complex: there were numerous trees; the grass was allowed to grow freely and tended to form tussocky clumps; one side had a small stream cutting across, while the other had a deep man-made pond.

2.1.1.2. *Shelters*

Each half of the enclosure was supplied with 4 wooden boxes to act as shelters; these structures were approximately 2 metres by 1 metre, and were kept replenished with clean straw several times a year. The shelters, or Huts as they are often referred to in the study, were raised off the ground using 0.5 metre wooden stilts to keep them dry, and each entrance was accessed by means of a wooden ramp. The back of each hut was constructed to allow maintenance of the bedding, and had a folding flap which could be secured to maintain a weather-tight space. These flaps also allowed an observer to keep a regular watch on the progress of litters; it was not possible, however, to leave the flaps open during observation sessions (in order to record more detailed information about

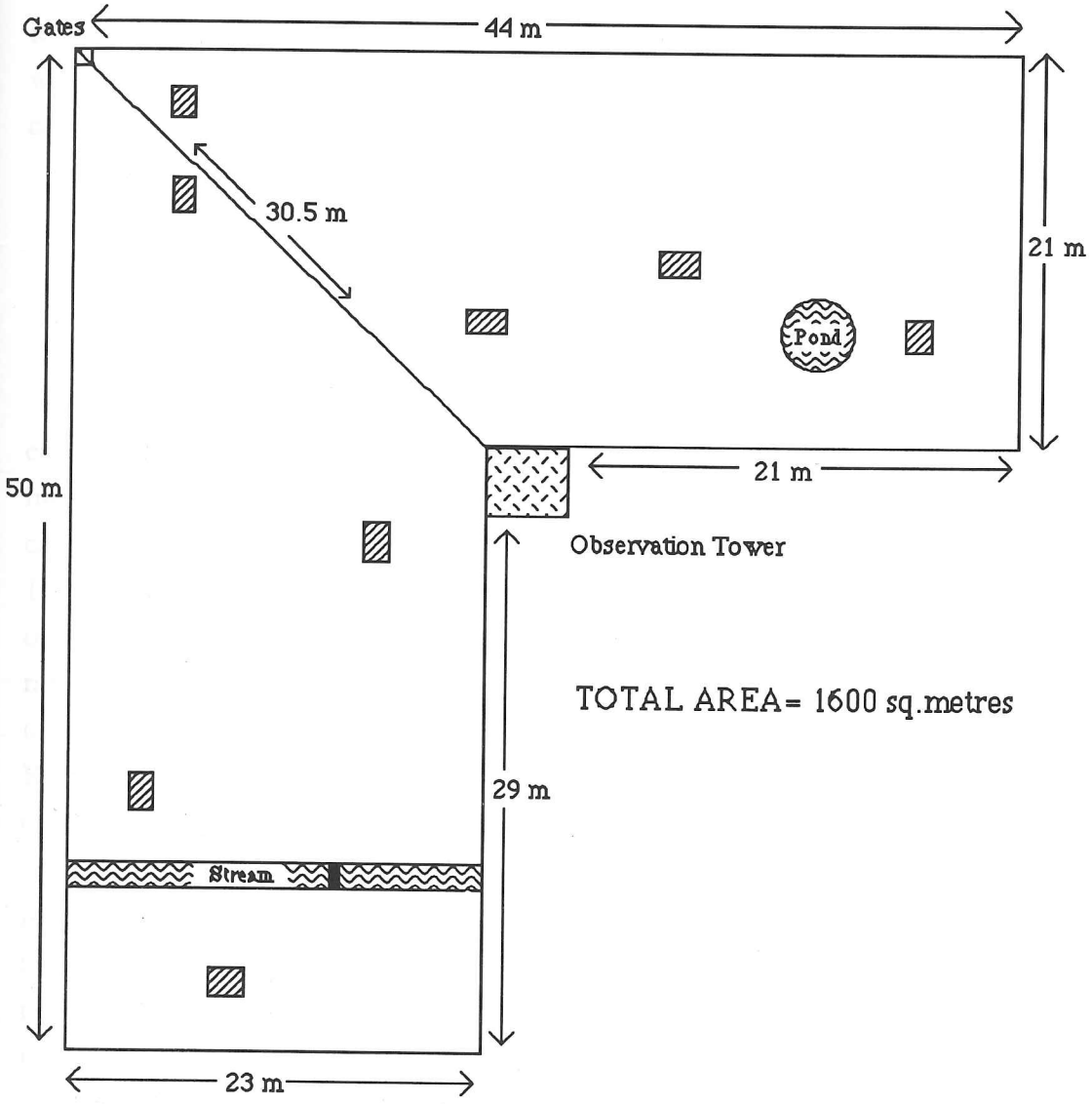


Figure 2.1: A Schematic Plan of the Outdoor Cat Enclosure. The two sides were separated by the diagonal fence; hatched boxes indicate the approximate position of the wooden shelters or "Huts" in each group. The "Gates" in the upper left corner mark the entries to each side of the enclosure, and food was left in this region of each side.

mother-litter and other interactions) due to the detrimental effect of weather and the undue lack of privacy (often a major consideration when choosing a nest site). The huts were primarily intended as places for females to rear litters of kittens. They also provided an important means of shelter for all the cats in rain and winter conditions, remaining dry both inside and underneath. The number of nest boxes provided (e.g. 4 huts for each cat group) was not found to be a limiting factor and did not affect the welfare of kittens born into the colony. The analysis of kitten mortality and nest site is given in Section 5.9.

2.1.2. THE ANIMALS

2.1.2.1. *Group Structure*

Each separate cat "colony" was established in April, 1987, by a group consisting of an adult male and five breeding females (Table 2.1). The structure was intended to roughly mimic that seen in a number of previous studies on semi-feral farm cats, in which there is a group of resident females (2-7), regularly visited by a tom (Dards 1979; Liberg 1981). Because the absence of human interference was a primary condition of the study, it was decided to include the male as a resident member of the population, rather than introducing and re-capturing him on a seasonal basis. In fact, it is not so unlikely that many farm groups have permanent male members (Dards 1979; Liberg 1981; Kerby 1987). All the founding members were vaccinated against feline diseases, including cat influenza, during the first year of the study.

Several features added complications to the initial design. The first was the issue of individual relatedness; a large proportion of studies have noted that female groups are matrilineal, and consist mainly of kin who remain in the natal area. It was not possible to use sisters, mothers and daughters, or other kin relationships, due to an absence of related adults in the original cat colony at Madingley. Only Poppy and Pansy were related (sisters). There was a suggestion that Molly might be joined by her sister (Mandy), but unforeseen problems forestalled that eventuality. The cats that founded the outside groups were not chosen randomly, but were selected by Paul Heavens, using several criteria. They had to be of known breeding ability, either having bred successfully prior to the study, or of healthy, viable background; also, the cats to be introduced outside would need to be able to adapt to new surroundings, so timid or hyperexcitable individuals were deemed unsuitable (as it was suspected that they would either escape or become behaviourally abnormal). Despite the lack of kinship ties, the females had a common background, having inhabited a large shared area in the indoor breeding colony with other females over the two or three years prior to this study.

Table 2.1: Founding Members of the Cat Study Groups

Name	Sex	Date of Birth	Date of Release	Side
Trossachs	Male	1/6/81	15/4/87	A
Katrina	Female	1/6/85	29/4/87	A
Becky	Female	1/6/83	16/4/87	A
Tessa	Female	1/7/83	16/4/87	A
Pansy	Female	9/1/84	15/4/87	A
Poppy	Female	9/1/84	13/5/87	A
Zac	Male	29/6/82	15/4/87	B
Jenny	Female	1/2/83	16/4/87	B
Calico	Female	1/6/83	16/4/87	B
Wanda	Female	1/6/85	7/5/87	B
Laura	Female	Pre-1976	29/4/87	B
Molly	Female	1/6/83	20/4/87	B
Daisy	Female	3/8/85	15/4/87	B

A second minor complication was the addition of a mature non-breeding female, Laura, to one group. She was known to be unable to reproduce, after a long history of successful litter-rearing, and was thought unlikely to have much influence on the group. In fact, she did not breed during the study, but played a surprising and unexpected role as an allomother for many litters.

2.1.2.2. *Identification*

It was generally simple to identify individuals just on the basis of coat colour. Where there were several similar cats, size and body build were useful criteria. In the last year of the study, it became somewhat more difficult to distingish certain individuals, and then more detailed aspects were used for identification: eye colour, lighter or darker colour hues, dark stripes down the back, and unique features (e.g. a blind eye, as in Pippin; Table 2.2). Often the naming of new cats would refer to a distinguishing feature (e.g. a pale mustardy ginger named Dijon). The main difficulties were with black males (Side B), ginger kittens and tabbies (both Sides A and B), but it was rarely the case that an animal could not be identified. Where a glimpse was too fleeting to positively name the individual, the data were not included. Names were reduced to the first three letters (or four if necessary) for the purposes of data recording.

When kittens were born, they were fully described and named (where possible), and a list was kept at hand during watches until they could be reliably identified without such an aid. The first letter of the mother's name determined the first letter of her kittens' names (e.g. Calico had Carbonel, Catkin, Columbus, etc.); all identified animals were given names. The individual cats named throughout the thesis are presented in Figure 2.2, with matrilineal connections, sex-class, and birth year (for younger cats) indicated.

2.1.2.3. *Demography*

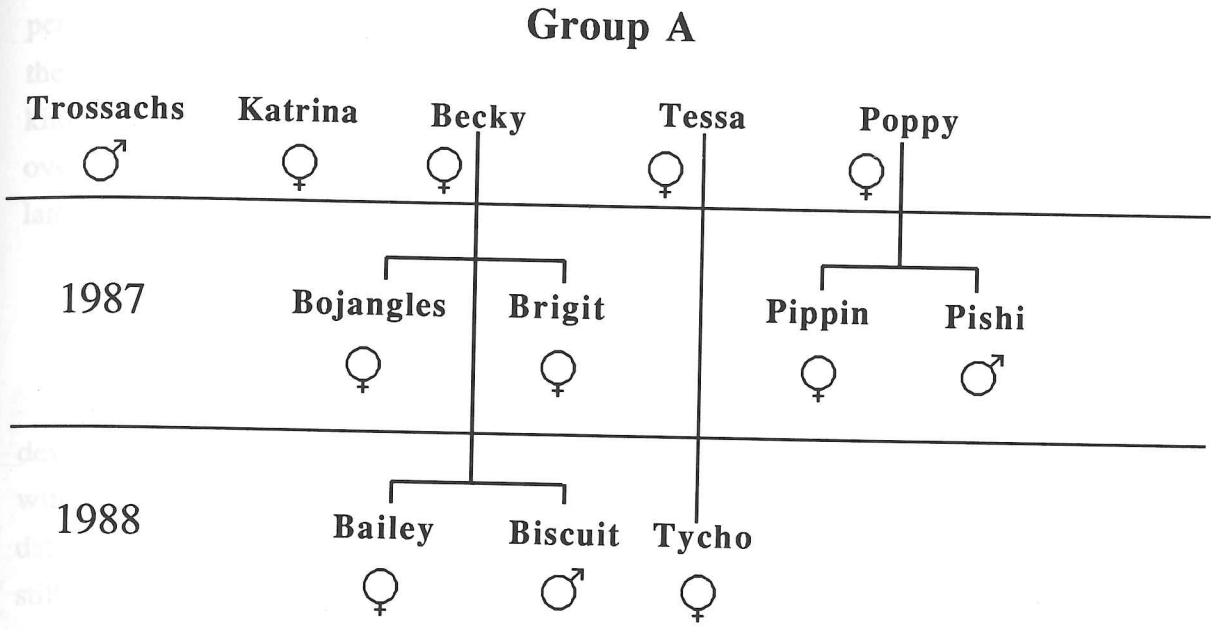
As mentioned, each group was founded by a mature male and five breeding females (supplemented by the non-breeding female, Laura, on Side B). In 1987, the year the cats were released into the enclosure, 22 kittens were born on Side A and 19 on Side B. Due to the incidence of cat influenza and the lack of maternal care by some females, only 9 kittens survived to increase colony numbers. At the start of 1988, Side A had 10 individuals (8 females, 2 males) and Side B had 12 members (7 females, 5 males); 20 kittens were then born on Side A and 29 on Side B. At this point, the actual density was 50 surviving cats in the whole colony; it was felt to be dangerously high for the purposes of the study, and, on the advice of the Home Office Inspector, the young cats born in 1988 were removed and re-homed. However, a total of 7 young cats managed to evade the

Table 2.2: Description of Individual Cat Members of Each Group

Name	D.O.B.	Mother	Father	Sex	Side	Description
TROSSACHS	1/6/81			M	A	black
KATRINA	1/6/85			F	A	grey tabby
BECKY	1/6/83			F	A	tortoiseshell
TESSA	1/7/83			F	A	ginger
PANSY	9/1/84	Penelope	ZAC	F	A	brown tabby
POPPY	9/1/84	Penelope	ZAC	F	A	dark tabby
n=4	4/5/87	TESSA	ZAC		A	?
n=?	9/7/87	TESSA	TROSSACHS		A	?
n=3	15/7/87	BECKY	TROSSACHS		A	2 tortoiseshell, 1 tabby
BUTTONS	15/7/87	BECKY	TROSSACHS		A	black
BOJANGLES	15/7/87	BECKY	TROSSACHS	F	A	black & white
BRIGIT	15/7/87	BECKY	TROSSACHS	F	A	tortoiseshell & white
n=1	17/7/87	POPPY	TROSSACHS		A	?
PIPPIN	17/7/87	POPPY	TROSSACHS	F	A	tabby & white, blind in one eye
PISHI	17/7/87	POPPY	TROSSACHS	M	A	dark tabby & white
n=5	6/12/87	POPPY	TROSSACHS		A	2 black, 1 tabby & white, 2?
BISCUIT	24/4/88	BECKY/TESSA	TROSSACHS	M	A	small ginger
TABASCO	24/4/88	BECKY/TESSA	TROSSACHS	M	A	larger ginger
TIGGER	24/4/88	BECKY/TESSA	TROSSACHS	M	A	small ginger & white
BASIL	24/4/88	BECKY/TESSA	TROSSACHS	M	A	large ginger & white
TABBY	24/4/88	BECKY/TESSA	TROSSACHS	M	A	tabby
BRETT	24/4/88	BECKY/TESSA	TROSSACHS	M	A	dark tabby
BAILEY	24/4/88	BECKY/TESSA	TROSSACHS	F	A	tabby, white chin & belly
TYCHO	24/4/88	BECKY/TESSA	TROSSACHS	F	A	dark tortoiseshell, ginger head-blotch
BLAZE	24/4/88	BECKY/TESSA	TROSSACHS	F	A	dark tortoiseshell, ginger nose-stripe
BAST	24/4/88	BECKY/TESSA	TROSSACHS	F	A	dark tortoiseshell, half ginger face
TREACLE	24/4/88	BECKY/TESSA	TROSSACHS	F	A	dark tortoiseshell
n=2	16/5/88	POPPY	TROSSACHS		A	1 "dark", 1 ?
PETUNIA	16/5/88	POPPY	TROSSACHS	F	A	black, white throat
PRUDENCE	16/5/88	POPPY	TROSSACHS	F	A	black
n=2	20/5/88	KATRINA	TROSSACHS		A	1 white, 1?
KORKY	20/5/88	KATRINA	TROSSACHS	F	A	grey tabby
n=2+	29/9/88	TESSA	TROSSACHS		A	?
n=1+	23/10/88	POPPY	TROSSACHS		A	tabby
n=4	21/4/89	POPPY			A	"dark"/tabby
n=7	22/4/89	TESSA			A	2 ginger, 2 tortoiseshell, 3 tabby
BRONTE	23/4/89	BECKY		F	A	larger black
BONIFACE	23/4/89	BECKY		F	A	black & white
BALLOU	23/4/89	BECKY		F	A	black & white
n=1	23/4/89	PIPPIN			A	?
PUFFIN	23/4/89	PIPPIN		F	A	black & white
BIBI	30/4/89	BOJANGLES		F	A	black & white
BREWSTER	30/4/89	BOJANGLES		M	A	tabby
BOBBIN	30/4/89	BAILEY		M	A	black
BUDDHI	10/7/89	BECKY		F	A	tabby
BALTHASAR	10/7/89	BECKY			A	tabby
BRUNELLA	10/7/89	BECKY			A	ginger
BRIOCHE	10/7/89	BECKY		M	A	ginger, white face
n=1(+?)	17/7/89	TESSA			A	ginger
POLLY	23/7/89	POPPY			A	tabby
PUSHKIN	23/7/89	POPPY			A	tabby

Name	D.O.B.	Mother	Father	Sex	Side	Description
PICKLE	23/7/89	POPPY			A	tabby
PEPITA	23/7/89	POPPY			A	tabby
POTLATCH	23/7/89	POPPY			A	black & white
PUMPERNICKEL	13/9/89	POPPY			A	black
ZAC	29/6/82			M	B	tabby
JENNY	1/2/83			F	B	ginger & white
CALICO	1/6/83	Calypso	Simon	F	B	grey & white
WANDA	1/6/85			F	B	black & white
LAURA	Pre-1976			F	B	dark tabby
MOLLY	1/6/83			F	B	ginger
DAISY	3/8/85	Dixie	TROSSACHS	F	B	dark tortoiseshell
n=2	21/6/87	CALICO	ZAC		B	2 tabbies
CARBONEL	21/6/87	CALICO	ZAC	M	B	black
CATKIN	21/6/87	CALICO	ZAC	M	B	brownish tabby
n=1	22/6/87	DAISY	ZAC		B	tabby
DIJON	22/6/87	DAISY	ZAC	M	B	pale ginger, white moustache
DOOLITTLE	22/6/87	DAISY	ZAC	M	B	paler tabby
n=2	24/6/87	MOLLY	ZAC		B	?
MULBERRY	24/6/87	MOLLY	ZAC	F	B	dark tortoiseshell
n=4	24/6/87	JENNY	ZAC		B	?
n=5	29/9/87	JENNY	ZAC		B	ginger & white
n=1	25/3/88	CALICO	ZAC		B	black
COLUMBUS	25/3/88	CALICO	ZAC	M	B	black
CLEO	25/3/88	CALICO	ZAC	F	B	tabby & white
CASEY	25/3/88	CALICO	ZAC	M	B	tabby
CAMILLE	25/3/88	CALICO	ZAC	F	B	tabby & white
n=4	25/4/88	JENNY	ZAC		B	1 tortoiseshell, 3?
DUFFY	1/5/88	DAISY	ZAC	M	B	black
DINAH	1/5/88	DAISY	ZAC	F	B	tabby
DARWIN	1/5/88	DAISY	ZAC	M	B	ginger
DICKORY	1/5/88	DAISY	ZAC	M	B	pale ginger
DANDY	1/5/88	DAISY	ZAC	M	B	ginger, white chin
WYNN	6/5/88	WANDA	ZAC	M	B	tabby & white
WEBSTER	6/5/88	WANDA	ZAC	F	B	tabby, white chin
WILBUR	6/5/88	WANDA	ZAC	F	B	tabby
WETZEL	6/5/88	WANDA	ZAC	F	B	black
n=2	9/5/88	MOLLY	ZAC		B	?
MIRA	9/5/88	MOLLY	ZAC		B	dark tortoiseshell, long hair
n=4	12/7/88	JENNY	ZAC		B	ginger & white
n=?	8/9/88	CALICO	ZAC		B	?
CHAUCER	26/3/89	CALICO		M	B	black & white
CHARLOTTE	26/3/89	CALICO		F	B	tabby
n=3	11/4/89	JENNY			B	1 ginger & white, 1 tortoiseshell & white, 1 ?
MAEVE	25/4/89	MOLLY			B	dark tortoiseshell
n=2	30/4/89	MULBERRY			B	?
MAGOG	30/4/89	MULBERRY			B	tabby
n=2	16/5/89	WANDA			B	2 tabbies
n=?	3/7/89	JENNY			B	?
n=?	3/7/89	CALICO			B	?

N.B. Where listing is '?', this indicates one of several things; if under "Name", then the kittens died soon after birth and were not named individually, or the littersize was unknown. If under "Description", then this corresponds to kittens that disappeared soon after birth. Where parentage or sex was not known, this entry is blank. Capitalised names refer to cats in the present study.



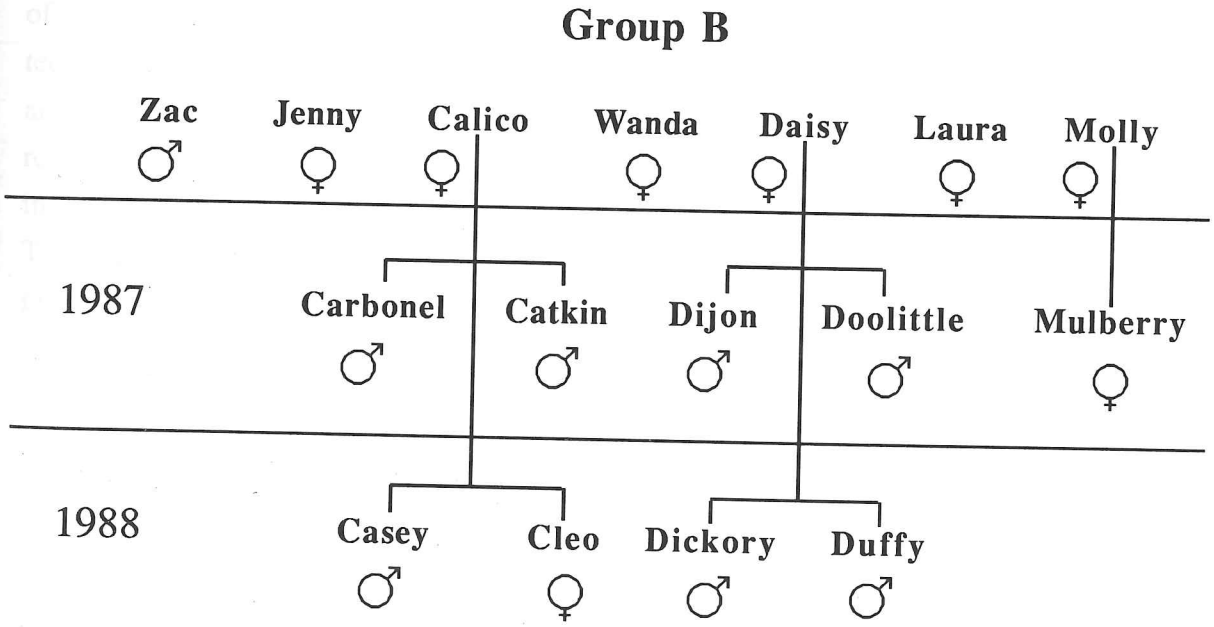


Figure 2.2: The focal members of the cat groups in the study. Vertical lines indicate lineages and connect mothers with offspring Horizontal lines link littermates. (a) Group A; (b) Group B.

persistent attentions of the trap, and were incorporated into the study population, bringing the total to 13 on Side A (10 females, 3 males) and 16 on Side B (8 females, 8 males). 31 kittens were born in Side A in 1989, and 19 in Side B. With high levels of kitten mortality over the summer, due to an outbreak of cat flu', the population by the end of the study in late 1989 was relatively unchanged from that at the start of the year (Figure 2.3).

2.1.2.4. *Categorisation of Age Groups*

General age groups were distinguished in order to look at broad developmental differences in social behaviour. Kittens were defined as individuals born within the calendar year, usually aged from birth to a maximum of 9 months (where the date of birth was particularly early). Juveniles were individuals born the previous year and still non-breeding, while adults were those cats at least 2 years old or breeding. In practice, it was very straightforward; those cats born in the first breeding season, 1987, failed to breed themselves until 1989. They were considered "Juveniles" during 1988 Focal and Proximity observations. In 1989, they assumed "Adult" status. Individuals born in 1988 were "Kittens" for that year, becoming "Juveniles", and in some cases, "Adults" in 1989 (e.g. Tycho and Bailey). Other authors have used definitions based mainly on average age of maturity and the display of mature breeding behaviour (Natoli 1985; Kerby 1987); this technique was not optimal for the study population, as cats born into the colony, female and male, failed to show any mature breeding or scent-marking behaviour until 1989. As a result, the category "Juvenile" was used as a blanket term for those cats born in 1987 (who initially bred in 1989); "Sub-adult" or "Immature" might be equivalent optional terms. Throughout the study, "Juvenile" refers to a specific set of 9 cats for 1988; they were grouped as "Adults" for the observations of 1989.

2.1.3. FEEDING

2.1.3.1. *Provisioning*

The groups were fed twice daily, around 9 am and 2 pm, during the week and once, around 10 am, on the weekends; all feeding was done by a technician, usually Paul Heavens, to prevent the observer's appearance becoming associated with feeding. This greatly facilitated the process of habituation, and the cats rapidly came to ignore the observer during daily watches. The food given was Whiskas Supermeat cat food (assorted flavours, dependent upon availability) mixed with Purina dry cat chow, all provided by Pedigree Petfoods; the amount was initially calculated per cat, commensurate with the amount given to cats in the indoor colony (roughly 400 grams per animal, plus dry food).

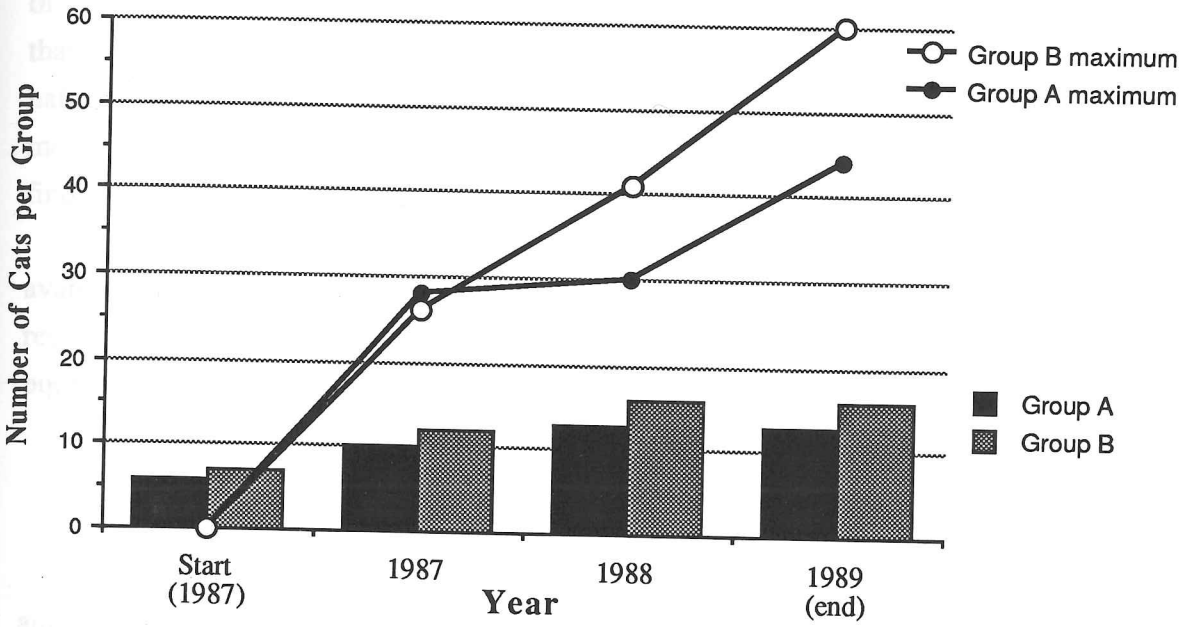


Figure 2.3: The demography of the two cat groups from 1987 to 1989. Columns indicate the actual size of each group, starting with the original founding adults, and including permanent group members each year. Lines show the maximum potential for growth, based on the number of kittens born each year plus members from the previous year.

It became apparent that a free-ranging lifestyle demanded larger amounts of food, and quantities were increased such that food dishes were rarely empty, to prevent any changes in behaviour due to food stress or competition. On the recommendation of Andrew Jagoe, a veterinarian, the cats were regularly de-wormed through the artifice of medication mixed into the food supplied.

The decision to regularly feed the study cats was based on the limitations of the enclosure and the expectation of a burgeoning cat population; it did not seem realistic that sufficient prey would pass through the enclosure, especially considering the fact that half the boundaries were provided by solid walls founded in concrete, a sure deterrent to most rodents. Any food restriction, whether active or passive, would have skewed the findings or had still more drastic effects.

Water was also provided at all times; a large (1.0 m x 0.5 m) water tray was available in each side of the enclosure, in the general feeding area by the door. These were replenished regularly. In addition, cats often used the natural water sources available in all but the dryest weather, the pond in Side A and the small stream in Side B.

2.1.3.2. *Captured Prey Food*

Despite the regular provision of large quantities of commercial cat food, the animals in the study continued to hunt and supplement their diets. Captured prey included both edible and inedible species, as indicated by the circumstances after capture. Inedible prey included the common mole (*Talpa europaea*) and the common shrew (*Sorex araneus*). Edible species, such as the common vole (*Microtus arvalis*), the blackbird (*Turdus merula*), the house sparrow (*Passer domesticus*) and the red-legged partridge (*Alectoris rufa*) were identified, but many individual prey were unrecognisable from the remains (scattered feathers or lone tails), if any remains were left at all. The cats probably consumed representatives of several other rodent and bird species which were not identified. Individuals were also observed actively chasing and hunting many insects, including butterflies and some dipterans; these prey were less frequently caught or consumed.

2.2. DATA RECORDING

2.2.1. PROXIMITY DATA

Proximity to other individuals was recorded for each Adult individual from January 1988 to June 1989, using an Instantaneous scanning method of sampling. This was not a measure of nearest neighbour, but noted the distance between the Focal

individual and all other Adult and Juvenile cats in the group. Five major categories were considered: Contact, wherein two or more cats were in actual physical contact, often while resting; Less Than Fifteen Centimetres, in which cats were not in contact but were obviously associating closely (this category was merged with the following one for the purposes of analysis, creating a new category called "Less than Thirty Centimetres"); Fifteen to Thirty Centimetres; Thirty Centimetres to One Metre; and One to Five Metres. Two other possibilities were also noted: Greater than Five Metres Away and Out-of-Sight. The distances were estimated by "eyeball" as imaginary concentric circles around each Focal animal. Although the closer distances appear unnecessarily accurate, they were chosen as the familiar measures, six inches and one foot, and the notional inches converted to metric equivalents for consistency of reporting. Several factors contributed to the initial decision to pool the two categories between Contact and Thirty Centimetres to One Metre; the first aspect was the extremely small sample sizes for Less than Fifteen Centimetres, which made the data difficult to handle along with the larger values in all other categories. The second reason was concerned with accuracy; given the large distance between the observer and the animals, the fine distinction between contact and less than fifteen centimetres seemed overly specific. The third, and perhaps most relevant, argument was that the differences between less than fifteen centimetres and fifteen to thirty centimetres were not biologically important for a species of this size (especially when considered along with the small sample sizes); it therefore seemed sensible to consider contact and then the pooled closer distances equivalent to less than thirty centimetres.

As the data were collected over a long timescale, it was decided to take a few daily recordings to keep the quantity of data to a manageable size. The other main constraint was the long-term nature of certain interactions (e.g. Resting/Sleeping in Contact, as discussed in Section 2.2.2); more frequent proximity recordings would have overestimated the Contact category when individuals slept for protracted periods together. Proximity was measured at the start of every watch, whether Focal or Maternal (Section 2.2.3), and at the end of every watch, if more than 1.5 hours long. A reasonable separation in time was a precaution to help ensure the relative independence of the two recordings.

Proximity was recorded using specifically designed checksheets (e.g. Hinde 1973; Martin & Bateson 1986), as shown in Appendix A; these data were later summarised for each possible dyad at each distance category. From this, weekly, monthly, seasonal, yearly and dyadic totals could be found. Younger animals were recorded for the Focal Adults (e.g. mother and kittens), but were not used as Focal subjects themselves, as there were far too many individuals who were often difficult to distinguish for an instantaneous observation.

2.2.2. FOCAL BEHAVIOUR DATA

Focal Behaviour was recorded for all Adult and Juvenile cats from January 1988 to April 1989. Only those individuals designated at the start of 1988 were used as Focal animals. This included the two Adult Males, all Adult Females and the 1988 Juveniles (Bojangles, Brigit, Carbonel, Catkin, Dijon, Doolittle, Mulberry, Pippin and Pishi). A total of 34 categories were distinguished (see Section 2.3). The number of observations varied for each month (Table 2.3.a) and for each individual (Table 2.3.b), often depending on availability and visibility.

Checksheets (shown in Appendix A) were designed to use a combination of One-Zero and Continuous sampling methods, using the principles discussed in Hinde (1973). Each Focal animal was observed for 34 minutes, where the sample interval was 30 seconds, for a total of 68 separate observation periods. A battery-operated bleeper delivered a tone every 30 seconds to keep sample intervals constant. The total sample length was chosen after an initial pilot study (Section 2.3.1), in which it was commonly noted that activity was not contained to discrete and convenient human time concepts; it satisfied the observer's qualms about missing behaviour that might occur just after the end of a 30-minute watch. Thirty seconds was chosen as the sample interval after a trial period in November 1987 using 15-second intervals; the unduly rapid pace detracted from observer concentration and left more than half the checksheets blank. Initiator, Recipient and action were noted for all interactions involving the Focal individual.

One-Zero time-sampling was chosen over other possible methods because of the types of behaviour under observation; although it tends to give overestimates of duration and often fails to account for bout-type behaviour and frequency (Altmann 1974), there were strong reasons for using the method. Most behaviour patterns were infrequent or rare, as they were specifically concerned with social interactions, so Instantaneous or Scan sampling would have yielded much less information (Lee 1983c; Martin & Bateson 1986); some activities were fast-paced and involved several interactants, so that Continuous recording would have been unwieldy and eventually inadequate. In fact, with the modifications made for this study, One-Zero sampling was a workable and useful technique. Although the main data presented are concerned with the number of intervals in which a particular behaviour was seen, supplementary quantitative information is provided on the actual frequency of most patterns.

For each watch, a Focal animal was chosen. At first, it was thought to do this by means of a random number (animal) table; unfortunately, the designated animal was rarely one of the cats in sight at that time (by chance). Instead, the observer arbitrarily chose an individual in view at the start of each watch, avoiding those watched previously that day. Overall, most animals were observed for a roughly similar number of times,

Table 2.3.a: Monthly Numbers of Focal Observations

Month	Year	Side A	Side B	Total
November	1987	0	5	5
January	1988	14	11	25
February	1988	5	9	14
March	1988	13	12	25
April	1988	36	53	89
May	1988	19	39	58
June	1988	31	26	57
July	1988	31	37	68
August	1988	48	48	96
September	1988	0	0	0
October	1988	62	67	129
November	1988	44	55	99
December	1988	51	44	95
January	1989	67	72	139
February	1989	66	68	134
March	1989	91	87	178
April	1989	7	7	14
TOTAL		585	640	1225

Table 2.3.b: Number of Focal Observations on Individual Cats

Name	Sex	Side	Number
Trossachs	M	A	75
Katrina	F	A	66
Becky	F	A	72
Tessa	F	A	80
Pansy	F	A	64
Poppy	F	A	73
Bojangles	F	A	45
Brigit	F	A	35
Pippin	F	A	35
Pishi	M	A	36
Zac	M	B	69
Jenny	F	B	79
Calico	F	B	75
Wanda	F	B	78
Laura	F	B	65
Molly	F	B	79
Daisy	F	B	50
Carbonel	M	B	25
Catkin	M	B	21
Dijon	M	B	40
Doolittle	M	B	17
Mulberry	F	B	35

Table 2.3.b: Number of Focal Observations on Individual Cats

Name	Sex	Side	Number
Trossachs	M	A	75
Katrina	F	A	66
Becky	F	A	72
Tessa	F	A	80
Pansy	F	A	64
Poppy	F	A	73
Bojangles	F	A	45
Brigit	F	A	35
Pippin	F	A	35
Pishi	M	A	36
Zac	M	B	69
Jenny	F	B	79
Calico	F	B	75
Wanda	F	B	78
Laura	F	B	65
Molly	F	B	79
Daisy	F	B	50
Carbonel	M	B	25
Catkin	M	B	21
Dijon	M	B	40
Doolittle	M	B	17
Mulberry	F	B	35

depending on availability. After an initial period, when cats were watched regardless of Side (group), observations settled into a pattern designed to maximise and equilibrate Focal watches for the two groups. Each side was the Focal group on alternating days; in this way, it was often possible to watch every Focal cat in a group over the course of a day.

2.2.3. REPRODUCTIVE VARIABLES

The variables examined under the category of "reproductive" covered a range of elements. All factors surrounding the birth of kittens were noted (Table 2.4), including the Date-of-Birth (or an estimate if the kittens were found a few days after parturition), Littersize, Mortality of any kittens (the date and any identifiable causes), Mother's Age and Parity, the location and duration of occupancy of Nest Sites, and the Type of Care shown by the mother.

Another feature was a measure termed "Maternal Time Budget"; as nests proved to be inaccessible and predominantly invisible, the only rough indicator of maternal effort was the amount of time spent with kittens. Each mother was focally watched for two hours every day, from birth through to the end of six weeks. A checksheet was used (see Appendix A), and every five minutes an instantaneous scan of the mother was made. The location of the mother, her activity, and whether or not she was with her kittens, were noted, along with details of any other individuals within one metre of the kittens. Observations were made for all litters born from the start of the study in 1987 to the late summer in 1989. Only those litters which proved inviable due to early mortality were excluded.

2.2.4. OCCASIONAL OBSERVATIONS, OR FIELD NOTES

As well as the other data collection methods mentioned in the previous sections (2.2.1-2.2.3), Continuous notes were taken (see Appendix A) during all watches in 1988 and 1989. These included any currently non-Focal individuals, as Focal animals were accounted for through other means. The main contribution made by these data involved those rare and overtly noticeable activities (Lee 1983c), such as fighting and mating. The findings were an important supplement to the Focal Behaviour data. Also, in 1987, the only behaviour observations were in the nature of continuous field notes; these will be referred to in Section 4.6.

The information gathered in this way were not included in the main Focal analysis, as they were of a different type and were probably biased toward the more flamboyant actions (Altmann 1974).

Table 2.4: A Summary of Reproductive Variables

Name	Definition
Date of Birth	Litter birth date measured as number of days after January 1st each year.
Littersize-at-Birth	Actual number of kittens born in each litter, including stillbirths
Littersize	Number of kittens raised, discounting dead kittens from first 2-3 days after birth; Littersize-at-Birth minus stillborns and other early mortality
Communal Littersize	Total number of kittens when two or more litters combined
Parity	Number of litters for each mother as a measure of experience
Mother's Age	Counting from each mother's date of birth, in years
Type of Care (Care)	"Style" of caring for litters, e.g. Solitary or Communal
Number of Nest Sites (Nests)	Number of nests occupied by each litter over three time periods: the first three weeks after birth, the second three weeks after birth, and all six weeks following birth
Maternal Time Budget	As explained in Section 2.4.4.1, measured for each of the first six weeks after birth of a litter, and pooled for the first three weeks and all six weeks
Kitten Mortality	Percent mortality of each litter measured at the end of the first three weeks, the first six weeks and the first four months
Eyes Open	A measure of kitten development; the number of days after birth when most of the kittens in each litter had their eyes fully open (for the first time)
Mobile/Play	A measure of kitten development; the number of days after birth when kittens from each litter were first seen walking and playing inside the nest
Leave Nest	A measure of kitten development; the number of days after birth when kittens were first seen to leave the nest
Eat Solids	A measure of kitten development; the number of days after birth when kittens from each litter were first seen to consume solid food

2.3. BEHAVIOUR CATEGORIES

2.3.1. PILOT STUDY

After the introduction of the cats to the outdoor enclosure, regular observations were made in order to identify and describe the behaviour patterns which would be relevant to the study. The pilot investigation ran from April to September, 1987, during which time continuous notes of visible behaviour were made. As the primary focus of the study was social organisation, those patterns which involved interaction were the main categories, although several maintenance activities were also included. An attempt was made to take observations over a representative portion of the day, so watches were scheduled in both the early morning and the evening (until dark), as well as during the day.

Based on these observations, it seemed best to avoid feeding times as they were periods of artificially high activity. The cats could hear the food being prepared in the cat house (the well-known phenomenon of attunement to the sound of tin-openers) and seemed to display agitation. The time of feeding was not absolutely constant and the anticipation period was of variable length, so a general guideline was to start watches at least 15 minutes after feeding, to allow activity levels to stabilise. The other aspect of feeding was the fact that a single site was used on each side; this was more a by-product of the provisioning by technicians than a purposive choice on the part of the observer; however, food dishes were deliberately large and allowed access to six or more cats at a time. It may also have created a situation which more closely resembled the conditions in many colonies of similarly small size, such as farm populations. At any rate, to avoid sampling any artificial hierarchy established by the single food sources, it was thought best to withhold observations at feeding times.

2.3.2. CATEGORIES AND DEFINITIONS

A number of individual behaviour patterns were delineated and described; these were then assigned to larger, more general categories. After initially defining around 50 discrete actions, only a subset of these were actively included on the checksheets, and several more were eliminated as uninformative during the study. All those actions listed on the checksheets are defined below:

"General":Follow: One cat travels behind another, basically tracing its movements; this can be performed slowly or quickly, from close by or further back. It is shown by two or more animals taking a specific route quite close in time, or

more directly by a chasing behaviour ("Chase" was a subset of this behaviour). (FOLL)

Approach: One cat moves (locomotes) directly toward another cat, initiating a proximity closer than one metre with that specific individual. Several more detailed descriptions were incorporated into this definition, including a relaxed circuitous walk, a rapid and direct advance, and a more hesitant and crouched movement. (APPR)

Evade: Evasion or eluding involves one animal overtly drawing away from another, after having seen or directly encountered that individual. This action can be performed as running away (at high speed or while crouching) or by jumping back while facing the second cat, then walking or running further away. (EVADE)

Neutral: One cat approaches another (or mutual advance) and sniffs at it without touching; it then apparently ignores the other animal and often walks away (after Liberg 1984b). This category was later dropped from lack of observational data. (N^O)

Contact: **Sleep in Contact**: Two or more cats lie relaxed and asleep with their bodies touching to some extent. (SL/C)

Rest in Contact: Two or more cats remain resting (lying, sitting or standing) but awake while their bodies are touching. (RT/C) Because of the fine distinction between resting with eyes closed and sleeping, this and the previous pattern were pooled for analysis. (RT/SL/C)

Cheek or Head Rub: One or both cats (and sometimes more than two) touch their head and/or cheek on another individual. This can be directional or mutual, and may be repeated several times. (C/H/RUB)

Body Rub: One cat draws its body along the length of another animal. This behaviour often follows, or perhaps is initiated by, a cheek rub and precedes an anogenital sniff. Again, it can be directional or mutual. (B/RUB)

Close Sniff: One cat smells or places its nose on (or very near) another cat; this can involve nose to nose (nasonasal) contact or nose to anogenital region contact. It may be directional, or mutual as in so-called "greeting" behaviour (Dards 1979). (C/SNF)

Paw: One cat puts one or both forepaws on or toward another animal (e.g. onto a stump, log or hut upon which the other cat rests). (PAW)

Agonism: **Swipe**: One cat uses one or both forepaws and brings them in a rapid sweeping movement toward another animal. The paw is often cupped, with claws exposed. The action may be repeated, and may or may not involve contact. (SW)

Ear Flatten: Ears are drawn back horizontally, giving the head a flattened appearance; this action can be done to a range of degrees, from only slightly perked to completely flat against the head. (EFLAT)

Piloerection: Hairs on the nape of the neck, shoulder, back and tail are raised to give a fluffed-out appearance; in more extreme situations, there are a greater proportion of erected hairs. (PILO)

Tail Lash: The tail is switched back and forth repeatedly; this can be done slowly or rapidly, just at the tip of the tail or along the entire length. (TLASH)

Bite: One cat snaps its teeth at or succeeds in nipping another animal. (BIT)

Fight: A more exaggerated form of all the above actions, with rapid motions, often involving wrestling, biting, swiping and loud vocalisations. It is not often a prolonged behaviour, but tends to be brief and intense. (FIGHT)

Generally, agonism is behaviour used to warn off, force away, or actually harm another conspecific (Poole 1985).

Groom: **Self**: A cat licks, bites or scratches part of its own body. (GR/S)

Allogroom: One cat licks, bites or scratches the body of another individual. (GR)

Mark: **Scent**: A cat directs a fine spray posteriorly toward an object (e.g. log, tree, grass clump); this action is characterised (and distinguished from urination in males) by a vertical tail posture, the tip of which shudders back and forth. (MARK). Object Rubbing was later combined under the heading Scent-Mark, and is considered separately from social Rubbing and Spray-Marking.

Scratch: Cat claws the ground, trees, stumps or other objects with forepaws (after Tan and Counsilman 1985). (SCR)

Mate: **Mount**: One cat (invariably male) pounces on a second animal (usually female, but not always), holding the scruff of the neck in his teeth. The held animal may crouch, and the male will then stand on its back. Unsuccessful copulation attempts were recorded simply as "mounts". (MOUNT)

Copulation: A successful copulation attempt is signalled by a brief and obvious intromission, which includes a thrusting motion by the male and the more overt female response (below). (COP)

Female Response: The female cat has a stereotypic post-copulatory behaviour, which includes rapidly twisting around to swipe, loudly hiss and yowl at the male, then darting away. Both male and female cats groom themselves (anogenital region) after copulation. (FEMRESP)

Mating involves a series of behaviour patterns associated with reproduction. Many attempts are unsuccessful, often due to the lack of female tolerance when males initiate mating outside the receptive time of oestrus. The prelude to

mating includes female oestrus behaviour, with much vocalisation and sometimes lordosis and rolling (Kleiman & Eisenberg 1973; Poole 1985), and prolonged close following of the female by a male (often with his nose to her anogenital region).

Nurse: A female allows kittens to suckle on her nipples; they can be her own kittens (NURS) or those of another female (AlloNursing) (ALLONURS). This behaviour was considered to be generally indicative of lactation, although kittens are known to nurse on dry nipples.

Play: **Object**: An animal focusses attention on an object and manipulates it in an apparently "nonfunctional" and often exaggerated manner; the object is often a twig, leaf or insect. (O/PY)

Social: One animal interacts with one or more other conspecifics (usually involves one or more kittens) such that activities (e.g. chasing, fighting, mating) are removed from their normal social context; behaviour is often rapid and exaggerated. (S/PY)

Vocalise: **Meow**: A plaintive sound made through an "O"-shaped mouth with lips spread back slightly. (M)

Yowl: A drawn-out version of a meow, with a rising and falling tone. (Y)

Call: Repetitive yowling utterances. (C)

Brrr: A faintly questioning, rolling sound, often accompanied by rising tone. (BR)

Hiss: A drawn-out "sss" sound, or "chhh" warning sound. Often complemented by "spit", a sudden, short, exhaled sound. (HS)

Pant: A shortened, often repeated version of a hiss; "chhh, chhh, chhh". . Not often recorded. (PANT)

Growl: A deep, rolling throaty (or chesty) sound, often accompanied by agonistic gestures. (GW)

Purr: A low, grumbling tone from the chest; heard primarily in an affiliative context. (PR)

Further actions that were defined but not used (because of the lack of a social interaction in the pattern) are included in Appendix B. They were often the basis for qualitative description used throughout the study, especially the terms "Pace" and "Patrol".

2.4. DATA ANALYSIS

All of the statistical analysis discussed in this thesis was performed using data worksheets and files on Apple Macintosh computers. Much of the preliminary data was treated with the Excel™ and Statview 512+™ packages, while later tests and statistics were obtained using Statview 3.0™, which has slightly more sophisticated non-parametric abilities. Specific statistical tests are discussed and explained in the Methods sections of each data chapter; most of the data were treated non-parametrically, due to small sample sizes, skewed distributions, and the inefficacy of most transformation techniques on the particular data (Sokal & Rohlf 1981; Zar 1984; Martin & Bateson 1986).

The main results that will be presented are derived from Mann-Whitney U-tests (test statistic = U), Kruskal-Wallis tests (test statistic = H), Friedman's tests (test statistic = χ_r^2), and Spearman Rank Correlation (test statistic = r_s). All analyses were two-tailed, and significance was taken at the α= 5% level, such that "*" indicates a probability less than α= 0.05, "**" is a probability less than α= 0.01, and "***" is a probability less than α= 0.001. These symbols will be used in tables and figures throughout to designate statistically significant results. Figures show medians and inter-quartile ranges (first and third) as descriptive statistics, unless otherwise indicated. Throughout the data chapters, capitalised words refer to the variable factors relevant to the chapter.

2.4.1. CORRECTION FACTORS DUE TO AVAILABILITY

Several different sources of variation were distinguished in respect to individual availability. The first major aspect was the visibility of animals, due both to the structure of the enclosure and its observation tower, and to the movements of the animals. It was possible to account for this by listing cats as out-of-sight for Proximity and Focal watches. The second source was the number of watches done on each individual; this was also related to visibility and cat movements, and a summary was made for each animal (Table 2.3.b). The third, and least predictable, form of variation was the result of disease and mortality. Both Katrina (Side A) and Laura (Side B) were contributors to this problem. All three sources were taken into account when the data were weighted prior to analysis, and the weighting techniques are discussed for each separate form of data in the following sections.

2.4.2. PROXIMITY DATA

2.4.2.1. *Pooling of Data*

As an outcome of the sampling method for Proximity, two separate sets of scores were derived, one from the start of each watch, and one from the end (where the watch was at least 90 minutes long). In order to strengthen the totals, the two sets of data were compared to ascertain whether pooling was possible. A correlation analysis was performed whereby each set of numbers was weighted against the maximum total for that set of observations; this was done by multiplying each sum by the total number of observations made at the other time (e.g. [Contact 1] x [No. Observations 2]). The standardised values were then used in Spearman Rank Correlation analyses. The points were represented by each possible dyad. Results are tabulated in Table 2.5, such that the sum totals for observations number one and two for dyads showed a significantly linear association. In all subsequent analyses, the sums of the two sets of scores were used.

2.4.2.2. *Weighting for Individuals and Dyads*

The data were interpreted in several different ways, and each of the methods had specific weighting considerations. In the first case, data were entered as X-Y dyads, where X was the Focal individual; the factor here was determined by the number of observations with that Focal individual (Table 2.6.a). Secondly, data were considered as individual totals at each distance category, or the sum for X of all possible $X\text{-}Y_i$ dyads involving other Focal Adults and Juveniles; the weighting number was calculated from the number of observations for the Focal individual, multiplied by the number of appropriate and available dyadic combinations (Table 2.6.b). In the last method, data were entered as an overall total, at all distances less than five metres, for each individual. These values were weighted in a similar fashion to the previous instance, with the addition of a multiplicative factor (x 4) to account for the four separate distance categories which were pooled (Table 2.6.c).

2.4.2.3. *Out-of-Sight and Long Distance Observations*

A record was kept of the number of times that a particular individual was out-of-sight and when it was merely more than five metres away from all other individuals. The frequency of such instances varied from one cat to another, and are discussed with the other results of the Proximity analysis. These two categories allowed speculation about the nature of individual spatial relationships for those animals that were not often seen at closer

Table 2.5: Spearman Correlations for Pooling Two Separate Sets of Observations for the Analysis of Proximity Variables

Distance	**n**	r_s	**Z**	**p**
Contact	177	.834	11.061	<0.001 ***
Less than 30 Centimetres	177	.807	10.709	<0.001 ***
30 Centimetres to 1 Metre	177	.906	12.018	<0.001 ***
1 to 5 Metres	177	.943	12.516	<0.001 ***

Table 2.6.a: Weighting Factors For Dyadic Proximity Relationships

Name	No. First Watches	No. Second Watches	Total No. Watches
Trossachs	329	282	611
Katrina	254	207	461
Becky	329	282	611
Tessa	329	282	611
Pansy	329	282	611
Poppy	329	282	611
Zac	328	283	611
Jenny	328	283	611
Calico	328	283	611
Wanda	328	283	611
Laura	308	268	576
Molly	328	283	611
Daisy	328	283	611

N.B. All possible dyads involving Katrina adhere to the minimum found for Katrina (254, 207, 461), as do all the dyads with Laura (308, 268, 576).

Table 2.6.b: Weighting Factors for Individual Distance Totals. These calculations were performed to compensate for the effect of the independent absences of Katrina (from Group A) and Laura (from Group B).

Side A: (#dyads)(#observations) =

[(#dyads with Katrina)(#observations with Katrina present)] +
[(#dyads without Katrina)(#observations with Katrina absent)]

First Observation= [(12)(254)] + [(11)(75)] = 3873
Second Observation= [(12)(207)] + [(11)(75)] = 3309

N.B. For Katrina, totals are (#dyads)(#observations present) = 3048 and 2484

Side B: (#dyads)(#observations) =

[(#dyads with Laura)(#observations with Laura present)] +
[(#dyads without Laura)(#observations with Laura absent)]

First Observation= [(15)(308)] + [(14)(20)] = 4900
Second Observation= [(15)(268)] + [(14)(15)] = 4230

N.B. For Laura, totals are (#dyads)(#observations present) = 4620 and 4020

For example, Trossachs (Side A) was in Contact with other Adults for a total of 7 First plus 10 Second Observations. The weighted score for Contact would be the following calculation, summed over the two sets of observations: [(Observed total) / (Maximum score, from above)] x 1000

= [(7) / (3873) x 1000] + [(10) / (3309) x 1000]
= [1.8] + [3.0]
= 4.8

Table 2.6.c: The Weighting Factors For Individual Sums Over all Distances. These calculations follow immediately from Table 2.6.b, and continue to account for the absences of Katrina and Laura from a period of scan sampling.

Values = (No. of scans)(No. of possible dyads)(No. of distances [=4])

Side A: Maximum for First Observation = 15492
Maximum for Second Observation = 13236
Total Maximum = 28728

Katrina: First = 12192, Second = 9936, Total = 22128

Side B: Maximum for First Observation = 19600
Maximum for Second Observation = 16920
Total Maximum = 36520

Laura: First = 18480, Second = 16080, Total = 34560

proximities. They were subjected to the same weighting factors used to treat the main body of Proximity data.

2.4.3. FOCAL DATA

2.4.3.1. *Timing of Observations*

All Focal data were collected during daylight hours. Several abortive attempts to do night-watches suggested that it would be impossible to identify interacting individuals and the specifics of behavioural exchanges, even with the use of an image intensifier ("nightscope"). In addition, from the night observations that were made, it appeared that social interaction levels were no greater (and in fact probably much less) than those during the day.

The data were collected at a range of times during the day; when all watches were summed, there were peaks around 11:30 am and 3 to 3:30 pm, when the greatest numbers of observations were started (about 130 for each peak; Figure 2.4). Given this bimodal distribution, individuals were tested to ensure that there was no bias in the timing of watches involving any particular animal. Using a Kruskal-Wallis test, Focal cats were not found to differ significantly in respect to the distribution of the times at which they were observed ($H= 29.049$, $p= .113$, $df= 21$, $n= 1218$). Mann-Whitney tests were used to explore possible discrepancies between groups: overall, the two groups showed no significant difference from one another (Side A vs. Side B: $U= 176671.5$, $Z= -1.38$, $p= .168$), and no differences were seen between Adult Females and Adult Males ($U= 52468.5$, $Z= -1.223$, $p= .221$), or between Juvenile Females and Juvenile Males ($U= 9307.5$, $Z= -1.76$, $p= .078$). However, Adults and Juveniles had significantly different distributions ($U= 122514$, $Z= -2.371$, $p<0.05$), as did Females versus Males when all cats were included, due to the effects of age class ($U= 117927$, $Z= -2.723$, $p<0.01$); these changes were probably a result of the tendency for Juveniles to be less visible overall, so that watches in which they were the Focal individual had to be more opportunistic.

As a reflection of the differences in timing of Focal watches, Adults and Juveniles were generally considered separately.

2.4.3.2. *Number of Focal Watches*

As mentioned previously, the number of Focal watches differed for each animal (Table 2.3.b). An attempt was made to equalise the total number of watches for each Focal animal, but it proved impossible to overcome the effect caused by more

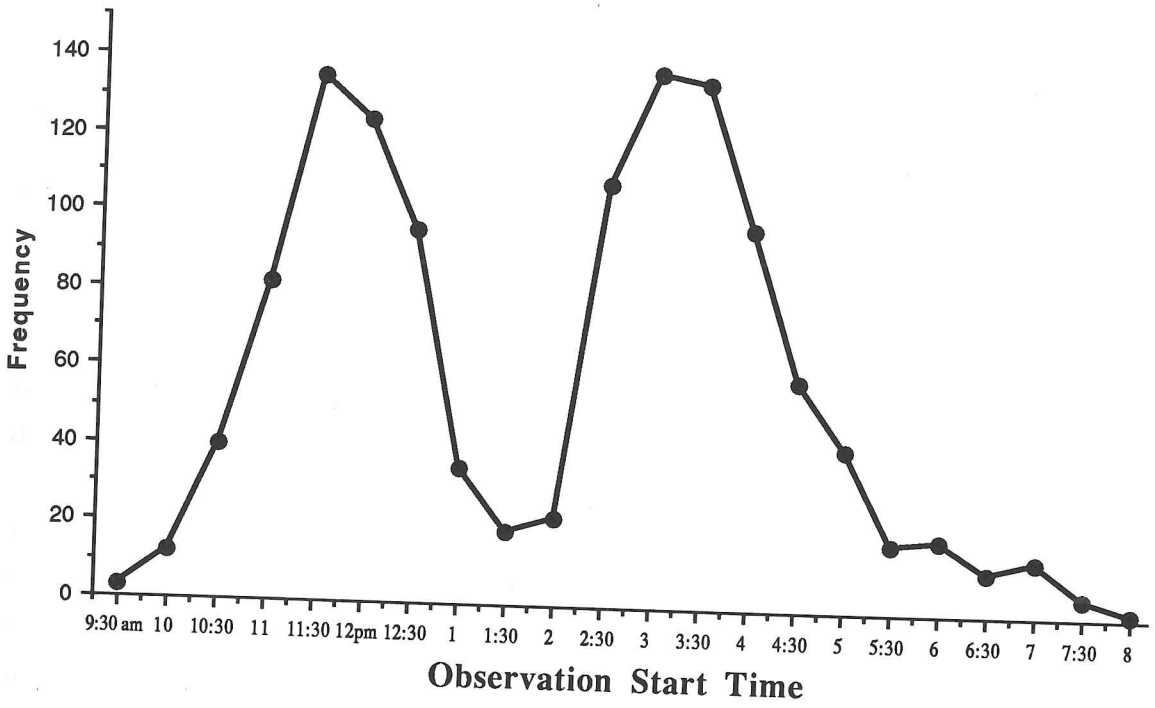


Figure 2.4: The starting times for all Focal observations. Focal data was collected throughout the day, but tended to peak once in the morning and again in the afternoon; the dip corresponds to the second feeding of the cats. Watches were 34 minutes long, and only the start time is given here.

reclusive individuals. As a result, the total number of observations was considered when the data were weighted for subsequent analysis.

2.4.3.3. *Duration of Focal Watches*

Focal watches were designed to be 34 minutes long, consisting of 68 30-second intervals. However, in practical terms, it was not feasible to keep all animals in sight at all times. This was partly due to the structure of the observation tower, in which the view was blocked by the angle of the windows and by the profusion of trees. As a partial measure to compensate for this problem, observations were made from the tower mainly in the winter; when leaves started to obscure the vantage point each spring, observations were made solely from within the enclosure itself. The other complication was the verdant habitat inside the enclosure, such that cats could travel into or through dense vegetation, to the detriment of the observer; this was a less constraining problem.

Intervals that each Focal individual spent Out-of-Sight (and therefore unrecorded in terms of interactions) were noted on the checksheets. When the Focal totals were found, the amount of observation time in sight was one of the factors used in weighting the data; this is further discussed in Chapter 4, and a summary of the visibility totals is presented in Table 2.7.a.

A second consideration was the weighting process itself; in order to compensate for the differences in numbers of watches and availability within each watch among individual cats, it was necessary to introduce several weighting factors to equalise the data. The possibility of sampling effects, in part due to the length of Focal watches (due to cat visibility), was investigated. The behaviour patterns seen every third and fourth month were summed for each individual; this included January-February 1988, April-May 1988, July-August 1988, October-November 1988, and January-February 1989.

The range of observation times for each pair of months was tested to ensure a similar distribution for each individual. No significant difference was found in the times each animal was observed (Table 2.7.b); using a Mann-Whitney test, no differences for morning versus afternoon watches were seen between Side A and Side B ($U= 176463$, $Z= -.409$, $p= .682$), Adults and Juveniles ($U= 175827$, $Z= -.622$, $p= .534$), Females and Males ($U= 171342$, $Z= -1.648$, $p= .099$) or Individuals ($U= 173247$, $Z= -.889$, $p= .374$). As a result, morning and afternoon watches were pooled for each animal, and behaviour rates were examined.

For each Focal individual, the rate of each separate behaviour pattern was found (i) when that animal was seen for all 68 observation periods in a watch, and (ii) when it was seen for less than all 68 intervals in a watch. These values were calculated by summing all observations of any behaviour for (i) and (ii) separately, dividing by the total

Table 2.7.a: Total Time for Individual Focal Observations, Giving the Number of 30-Second Periods and the Number of Hours Each Cat was the Focal Individual and In Sight

Name	Total No. of Periods	No. Out-of-Sight	Total in Sight	No. Hours in Sight
Trossachs	4928	378	4550	37.92 hr
Katrina	4454	326	4128	34.40 hr
Becky	4624	77	4547	37.89 hr
Tessa	5236	169	5067	42.23 hr
Pansy	4250	284	3966	33.05 hr
Poppy	4727	242	4485	37.38 hr
Zac	4420	212	4208	35.07 hr
Jenny	5329	282	5047	42.06 hr
Calico	4964	115	4849	40.41 hr
Wanda	5056	259	4797	39.98 hr
Laura	4216	327	3889	32.41 hr
Molly	5236	316	4920	41.00 hr
Daisy	3172	450	2722	22.68 hr
Bojangles	2958	178	2780	23.17 hr
Brigit	2414	83	2331	19.43 hr
Pippin	2244	267	1977	16.48 hr
Pishi	2448	93	2355	19.63 hr
Carbonel	1540	288	1252	10.43 hr
Catkin	1122	92	1030	8.58 hr
Dijon	2550	358	2192	18.27 hr
Doolittle	1122	43	1079	8.99 hr
Mulberry	2278	226	2052	17.10 hr

Table 2.7.b: Distribution of Focal Watches over Sampled Months, Using a Kruskal-Wallis test (x=Individual Cat, y=Time of Watch). Non-significant probability levels indicate no differences in the distribution of focal observation times across individual cats.

Months	df	n	H	p
January-February 1988	15	34	18.146	.255
April-May 1988	21	148	31.086	.072
July-August 1988	19	162	23.560	.214
October-November 1988	21	228	18.357	.626
January-February 1989	21	273	13.217	.901

Table 2.7.c: Spearman Rank Correlation Comparing Behaviour Rates for Complete versus Incomplete Focal Watches. Significant correlations indicate linear rank relationships regardless of watch length. Uncorrelated values correspond to rare behaviour patterns with many zero rates. All watches (both Complete and Incomplete) were pooled for subsequent analysis.

Behaviour	**n**	r_s	**Z**	**p**	
Follow	72	.234	1.973	<0.05	*
Approach	72	.314	2.645	<0.01	**
Evade	72	.095	.799	.424	
Rest/Sleep in Contact	72	.102	.862	.388	
Cheek/Head Rub	72	.346	2.918	<0.01	**
Body Rub	72	.217	1.831	.067	
Close Sniff	72	.245	2.061	<0.05	*
Paw	72	.190	1.602	.109	
Swipe	72	.188	1.581	.114	
Ear Flat	72	.253	2.134	<0.05	*
Piloerect	72	.326	2.747	<0.01	**
Tail Lash	72	.197	1.661	.097	
Bite	72	.272	2.295	<0.05	*
Fight	72	-.041	- .345	.730	
Mount	72	.136	1.148	.251	
Object Play	72	.050	.421	.674	
Social Play	72	-.020	- .165	.869	
Scratch	72	.083	.703	.482	
Spray-Mark	72	.601	5.068	<0.001	***
Nurse	72	.575	4.846	<0.001	***
AlloNurse	72	.535	4.504	<0.001	***
Groom Self	72	.227	1.913	.056	
AlloGroom	72	.482	4.059	<0.001	***

number of observation periods for each category, and multiplying each by 120 for an hourly rate. The shortest reliable time for a Focal watch was deemed to be 68 periods, as this accounted for the majority of cases, and allowed for the maximum degree of variation in the data.

Spearman Rank Correlation was performed to compare the performance rate of each behaviour when animals were seen for whole watches versus a proportion of total watch time. Most activities were significantly and positively rank correlated (Table 2.7.c); those that were not significant resulted from a preponderance of zero-scores (thus aligning the points along an axis) due to the rarity of the behaviour and its infrequent sighting. Therefore, it was decided to pool all watches, both for the activities that showed a strong correlation and for those rare patterns which were unlikely to be seen regardless of the length of watch (and which might only be seen in "incomplete" watches but not "complete" ones). The few behaviour activities that could not be accounted for in this way were Rest/Sleep in Contact, Scratch, and Groom Self. These actions could be performed while out-of-sight, which may account for the uneven distributions, and the latter two are concerned with maintenance; duration measures would probably be more relevant for these cases, as there could be no reason to assume constant rates of performance linked to watch length. Overall, sampling effects were not thought to be playing a role in the data findings, and all watches were pooled for subsequent analyses.

2.4.3.4. *Initiator Versus Recipient of Action*

To facilitate the analysis, it was decided to combine all occurrences of behaviour initiated by each Focal animal, regardless of the watch in which the observation was made. This meant that for the total findings in which, for example, Becky Approached Tessa, data were combined from Becky Focal watches and Tessa Focal watches, with that particular combination of initiator and recipient. As a result, the weighting factor was a sum of the total number of watches (and therefore visible intervals) in which each combination was possible. For some dyads, only one interactant was ever Focal, as for actions initiated toward (or by) Kittens and young cats born in 1988 and 1989; in these cases, the single source of information was provided by the Focal Adult involved. The outcome was a paucity of information regarding the interactions between Kittens and young Juveniles, but the addition of these individuals to the data pool would have tripled the number of dyads (already well over 150).

For each dyad, there were two elements: A to B and B to A (or A by B). This balance allowed the examination of asymmetry in dyadic relationships, as will be discussed at length in Chapter 4.

2.4.3.5. *Weighting for Individuals and Dyads*

It was explained previously in the chapter (Sections 2.4.3.2 and 2.4.3.3) that unequal numbers of Focal watches and amounts of within-watch visibility were obtained for each individual. These aspects were the source of standardising factors which were applied to all the raw data prior to final analysis. Through the weighting, it was also possible to compensate for larger effects, such as the early death of Katrina due to a ruptured pyometra, and the absence of Laura in November 1988 while recuperating from an operation for mastitis and mammary tumours (the tumours recurred in the spring of 1989, leading to the difficult decision to have Laura humanely killed just before the end of the study).

The maximum number of visible Focal intervals was calculated for each cat, and dyads were treated using the combination of the individual scores. Values were also found for individual totals (the sum of all possible dyads involving any one individual), weekly, monthly and "seasonal" totals.

2.4.4. DATA ON REPRODUCTIVE VARIABLES

2.4.4.1. *Time Budgets*

The general technique for collecting Time Budget data involved daily two-hour watches on each mother, from Birth to the end of six weeks. An instantaneous scan was made every five minutes, resulting in a set of seven scores (each with a maximum total of 25) for each week, such that a positive mark was added for each scan that the mother was with the litter. Daily totals were summed into weeks and then divided by the maximum possible score to find a percentage of the time watched that was spent with kittens. It was decided to approach the analysis using weekly scores, as daily totals fluctuated wildly, and often obscured the overall trend (which was much more clear on a weekly basis).

All analyses discussed in Chapter 5 were performed using the weekly percentage of time spent with the kittens. This was the only feasible way of obtaining some rough measure of maternal effort, as cats tended to use mainly invisible nest sites; it was possible, although requiring extreme attentiveness, to record all arrivals and departures from the nest as well as maternal presence. Because of the nature of the habitat, mothers were able to leave the nest and the kittens out of choice, as well as to feed and drink. Therefore, the time spent with kittens, or Maternal Time Budget, should be a relatively accurate reflection of the amount of effort a female chooses to "invest" in a litter (Kerby 1987). It was unfortunately impossible to record more precise physiological measures

such as rate of milk release or milk quality, so one underlying assumption was that there were no huge differences in the quality of nutritional care given while in the nest. Other forms of care, such as grooming and the provision of warmth, might compensate in some way if there were overall differences in lactation.

2.4.4.2. *Other Variables*

Most reproductive variables required the straight-forward noting of concrete elements, such as Date-of-Birth. Occasionally, of course, a small question arose if parturition occurred overnight or on a weekend with no scheduled watches. In these cases, it was necessary to examine the kittens and estimate their age (and Date-of-Birth) based on developmental changes like size, coat appearance and mobility. Littersize was also subject to problems in that kittens were sometimes cannibalised at birth. Most litters were uncomplicated and all kittens were present; a few litters were partially cannibalised, but often evidence remained that guided observational opinion (e.g. a part of a body). The few sources of uncertainty were the cases in which no kittens were found after a definite period of late gestation, and those in which a mother appeared to have an uncharacteristically small litter. In the case of Jenny, kittens rarely received care after birth, and were often deposited, still in the placental sac, at random points throughout the enclosure; despite attempts to search all possible places, there exists a small likelihood that a kitten or two was overlooked.

The complications with Littersize-at-Birth were part of the reason that the variable Littersize was derived; it deals with the actual number of kittens raised in a litter, and allows for neonatal mortality and cannibalism. Communal litters also provided a problem, as mentioned in Section 5.1. The uncertain element in true Littersize-at-Birth, as well as the high neonatal mortality, combined with the difficulties of accurately sexing young kittens without undue interference, made it impossible to calculate sex-ratio for litters. This was unfortunate, as there might have been influences on other reproductive variables, as well as some explanation for the skewing of the ratios in the surviving adult populations.

Kitten Mortality was calculated for each litter. Notes were kept when bodies were found or when litters suddenly decreased in size, and these were used to follow the history of any given litter. In most cases, the cause of death was logically surmisable; in other instances, the cause was unknown, and several intact bodies were sent for autopsy. The causes of Kitten Mortality will be discussed in Section 5.8.

Maternal Parity and Age were calculated from the records, based on known birth dates and prior litters. Nest Sites were recorded daily, and any change of location

was noted; this allowed the summary of nest sites, both numbers and locations, seen in Chapter 5.

2.4.5. OCCASIONAL OBSERVATION DATA

The data collected opportunistically were used to supplement the findings of the more thorough Focal watches. Because much of the behaviour under examination was infrequent but overt, it was possible to record most instances, where Focal watches might have been unlucky in timing and missed their occurrence. It was not feasible to weight these data, so they were not considered in the same pool as the Focal results. Instead, the sums were used as absolute frequency measures for inter-individual comparisons.

In addition, behaviour patterns were continuously recorded in 1987, before the advent of the Focal watches; these data were standardised for the amount of time spent watching (in minutes), and were separated into three sections: before the birth of kittens; during the rearing period; and in the "winter" prior to 1988.

2.4.6. WEATHER

The weather was recorded at the start of every watch, regardless of the type of data collection, and major changes were noted as they occurred. Over 1987, there was no apparent effect of weather on Maternal Time Budget, as indicated by preliminary tests. In fact, the presence of plentiful places to shelter meant that cats could take refuge without having to drastically modify their activity. Rain had the most noticeable effect, in that many individuals took shelter at the first drop, while others lay unmoving in the downpour, continuing whatever activity in which they were engaged. The swamp-like aftermath of the winter rains involved the flooding of lower areas, often burying paths in many inches of water and mud. Cats continued to traverse the paths, picking delicately around the puddles. The sun also brought change, prompting more indolent lazing in sunny spots.

Official weather statistics were obtained from the Boxworth Experimental Farm in nearby Elsworth, covering January 1988 through June 1989. Over the eighteen months of Focal and Proximity data collection, monthly temperatures and sunshine adhered to the monthly means from the past 39 years (Figures 2.5.a & b); however, monthly rainfall was atypical (Figure 2.5.c). Mean maximum and minimum temperatures were strongly positively correlated ($p<0.001$), as were temperatures with hours of sunshine (maximum: $p<0.001$; minimum: $p<0.05$) for each month. Cumulative rainfall was not linearly associated with the other weather variables. Proximity relationships were examined over separate months, and compared to the concurrent weather conditions. The results of the analysis are discussed in Section 3.5.3.

Figure 2.5.a

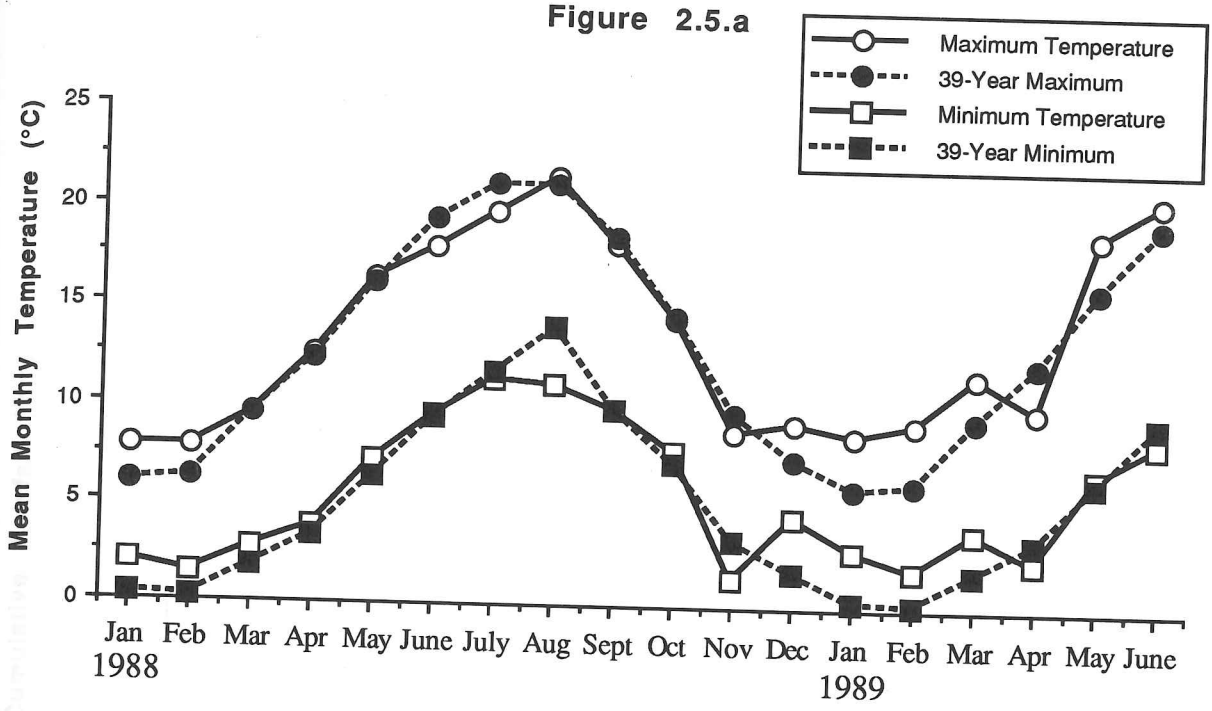


Figure 2.5.b

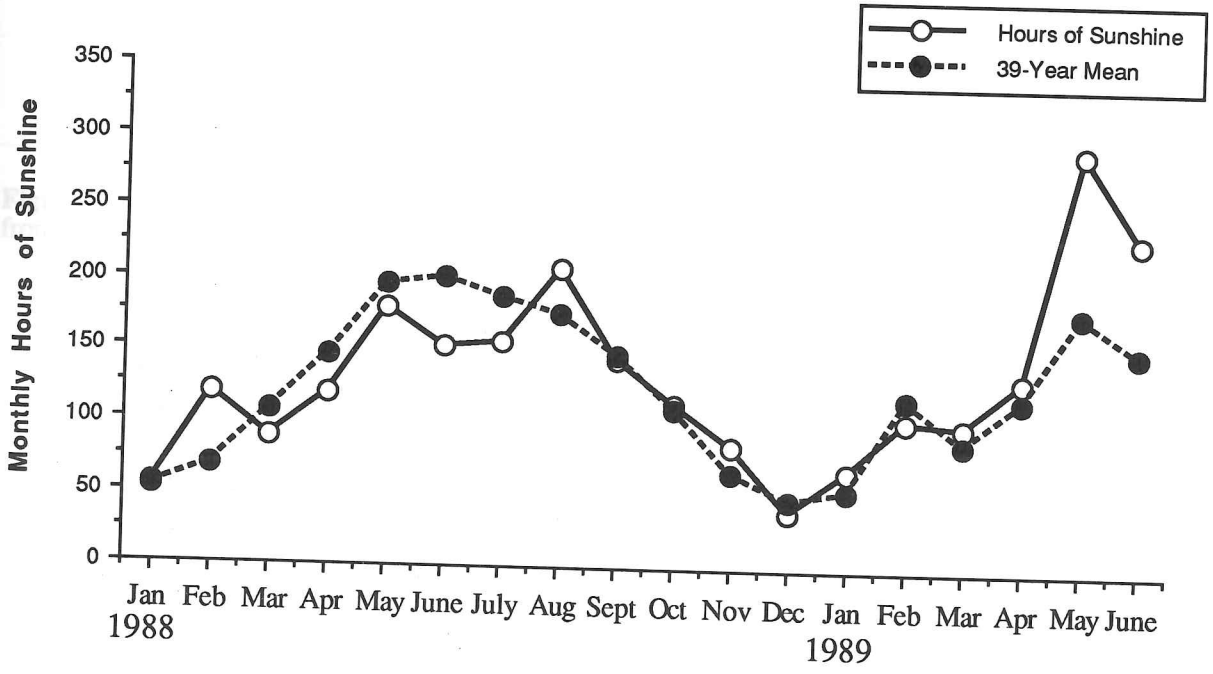


Figure 2.5: Monthly weather statistics over the eighteen month Focal period, compared with an average from the past 39 years. (a) Maximum and Minimum Temperatures; (b) Hours of Sunshine.

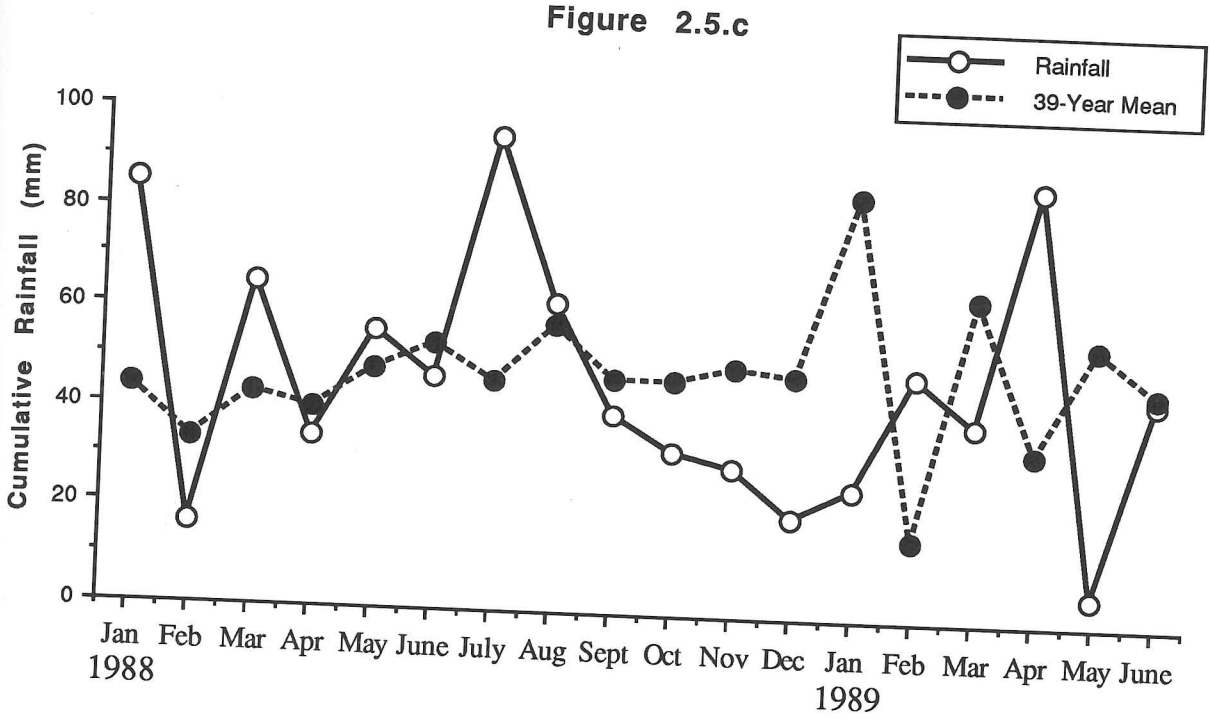


Figure 2.5: Monthly weather statistics over the eighteen month Focal period, compared with an average from the past 39 years. (c) Cumulative Rainfall levels.

An adult female, Daisy, in oestrus and rolling, with three adult males in attendance. The eldest male, Zac, is nearest Daisy, and his two mature sons (Dijon and Doolittle) are to one side. Two adult females are seen in the foreground. (see Section 4.4.2)

An adult female, Jenny, feeding (along with an adult male) after a day full of mating and rolling (in the mud). (see Section 4.4.1)

Chapter 3

Proximity Relationships

3.1. GENERAL INTRODUCTION

3.1.1. PREFACE

Before it is possible to examine the potential mechanisms (e.g. cooperation) behind the formation of affiliative groups, it is first necessary to establish the structure of the group. One of the first techniques which can be used to characterise the social structure of a population is the identification of spatial relationships (Fox 1975b; Hinde 1983; see Section 1.2.2.1). In cats, this has often taken the form of elucidating the use of home ranges and their sizes (see Section 1.2.1.3); however, given an established group, spatial differences can indicate much about the underlying social organisation. The information about the use of space can then be supplemented with details of behavioural relationships. This chapter investigates the proximity interactions between the various members of the groups in this study, while the next chapter (Chapter 4) examines the social behaviour associated with these spatial relationships. The term "proximity" is used interchangeably with both "distance" and "spatial" throughout the thesis, and is taken to mean "nearness in space" (Collins English Dictionary 1986).

Chapter 3 is divided into four major sections. The first three reflect the primary levels upon which social structures can be defined: the group organisation, the dyadic relationship component, and the individual members. The opening section (Section 3.2) addresses the colony as a whole, looking first for differences between the two study groups and then examining the influences of age and sex class on the spatial organisation; it is divided into the various age and sex categories to provide a clearer picture. The second section, The Dyad (Section 3.3), starts to examine the constituent relationships of the groups, in terms of pairs of cats; more detail is given regarding the major partners chosen for certain spatial associations. In a structured social group, spatial relationships are non-random and tend to involve specific pairs of animals (Kerby 1987; Kerby & Macdonald 1988); such partner "preferences" are elucidated in this discussion. The third part (Section 3.4) investigates the question of individual differences in the use of spatial relationships, and compares cats in their general availability for interaction and the distances they maintain from other conspecifics. The last main division (Section 3.5) deals with seasonal changes in spatial relationships; the question: "can proximity relationships be predicted from one reproductive season to another?" is asked as part of the search for the basis for group stability and behavioural associations.

The results presented in the first three sections, examining the separate levels of organisation, are necessarily overlapping; each part builds on the others due to the interwoven nature of social structure, wherein the individual affects the dyad, the dyad

affects the group, the group influences the individual, and so on. Sex and age classes are used throughout as a means of subdividing the colony into meaningful segments. To distinguish the members of the two groups and their relatedness, reference should be made to Figure 2.2.

3.1.2. METHODS

The general methods for data collection and for the treatment of numbers prior to final analysis were described in detail in Chapter 2. The results, taken from a total of 611 scans for most Adult individuals, were then separated into several distinct groups for the purposes of comparison. The first section of this chapter deals with overall colony structure, on the level of spatial relationships between different age and sex classes; all these categories were centred on Adults as the Focal subjects, as a direct result of the constraints on sampling a fluctuating population. Even when focussing on only Adult-other proximity, more than 7750 separate Focal observations were made, and each often involved as many as 25 possible interactants. The sum of all proximity scans (e.g. all conspecifics within a given distance) and all distances to other animals were used in this section, with the appropriate divisions by age and sex categories.

The second mode for analysis involved a consideration of dyadic relationships, primarily Adult-Adult and Adult-Juvenile. Some examination of Adult-Kitten spatial relationships was made, but this was reduced to a few individual Kittens, and own Kittens versus other Kittens, to simplify the problem. The data were in the form of weighted scan totals for each pairing combination.

Thirdly, individual cats were compared with reference to the overall totals found for each individual and each proximity category; observations of proximity greater than five metres from any other cat and out-of-sight were also considered. In this way, individual differences in the use of spatial relationships could be examined. For this section, data were the weighted totals from all scans for each Focal individual.

A further possibility, the presence of a seasonal component to proximity, is the subject of the last section in this chapter. Both monthly differences and those based on reproductive changes were considered. All dyadic sums (as for Section 3.3) and individual totals (as for Section 3.4) were the basis for analysis; these values were subdivided into seasons, using the method explained at the start of Section 3.5, and then weighted by the number of possible observations in the distinct "seasonal" periods.

As discussed in Chapter 2 (Section 2.2.1), it was deemed necessary to mix imperial and metric measurements; most similar studies have adhered to metric units and have used large-scale distances, with the smallest being "less than one metre" (Dards 1979; Kerby 1987; Macdonald et al. 1987). However, in this study, the combination of the

ability to make close-range distinctions and the limitations of the enclosure confines, suggested that units smaller than one metre were required. Unfortunately, SI units do not usefully cover the entire distance range examined in this study; for the smaller scale divisions, the choice lay between (roughly) fifteen and thirty centimetres or imperial units like six inches and one foot. From distant observation points, error-free distinctions are more difficult using centimetre units rather than inches (which are larger units). Therefore, the familiar lengths of six inches and one foot were used for data recording, but have been converted to metric units for more consistent data analysis and reporting. Thus, the proximity distances measured in this study are as follows: Contact, Less than Thirty Centimetres, Thirty Centimetres to One Metre, and One to Five Metres. The sum of these categories was also presented, as the Total to Five Metres.

Several forms of the data were used. The primary source of information came from each of the distance measures, and included a separate analysis for each value. When associations were found (Section 3.2.1), this enabled some data to be pooled; such combined measures were used to look at Adult-Adult interactions, particularly their commonest partners, as well as at individual differences, the pilot study of seasonality using months, and the effects of weather. In several parts of the chapter (Sections 3.2.2 and 3.3.1), analysis was first performed with all the distances to determine specific proximity patterns, and then lumped scores were used to examine more general trends with increased values. The third form of the data was used in Section 3.5, dealing with reproductive seasons. Due to the subdivision of scores into "season" units, the values at the two closer distances became even smaller; in order to compare the trends at all ranges, the closest two values were pooled again to create a "Near" score. However, in the absence of knowledge of whether middle or great distances would change with the seasonal units, the remaining distance measures were kept separate; the correlation done on intact measures (Section 3.2.1) would not necessarily apply to the data in its new form.

The terms "preference" and "preferred" apply to the examination of other cats seen within a certain distance of the Focal individual; they are used, as in similar studies (Kerby 1987; Macdonald et al. 1987), to indicate the dyadic combinations showing the highest proximity values. There is no imputation of active choice in the use of these words, but they facilitate the description of specific pairings with notably high proximity scores (or high social interaction levels, as in Chapter 4).

Friedman's analysis of variance was used for some of the analyses in this chapter and the following two data chapters. It is a non-parametric statistic that tests the difference (based on ranks) among three or more matched samples (Martin & Bateson 1986), and it looks for significant differences between the scores of several related samples. In the statistical package used, columns are treated as blocks in a randomised block-design, and they are ranked separately (Sokal & Rohlf 1981; Zar 1984). If

individual animals or behaviour patterns are entered as blocks, this test compares the distribution of ranks to see if they come from the same population of samples. Used in this way, the Friedman's test is somewhat unorthodox, however still valid if interpreted carefully. Where the ordered blocks (whether individual cats, distance categories or behaviour patterns) are given in addition to the test statistic, these are presented merely as an indication of the two extremes, but are not showing statistically significant differences between any two elements. The test statistic is given as χ_r^2 (Sokal & Rohlf 1981; Zar 1984). The Friedman's test can also be used to replace a repeated measures analysis of variance (Martin & Bateson 1986).

3.2. THE COLONY

3.2.1. FEMALE-FEMALE RELATIONSHIPS

The two groups of cats were compared for overall differences in proximity totals at each distance, but no discrepancy was found between the sides (Table 3.1.a). The two sexes were then compared; Males were found significantly more than Females at the greatest distance (Table 3.1.b) and tended to be seen more at long distances and less at close range. When different distances were tested against one another, observations in Contact roughly equalled those at Less than Thirty Centimetres ($Z= -.524$, $p= .600$), while Thirty Centimetres to One Metre ($Z= -2.9$, $p<0.01$) and One to Five Metres ($Z= -3.180$, $p<0.01$) had consistently higher values across all individual Adults. The longest distance gave higher scores than any other (Less than Thirty Centimetres: $Z= -3.180$, $p<0.01$; Thirty Centimetres to One Metre: $Z= -3.181$, $p<0.01$). Cats were also observed more often at greater than five metres than they were found to be out-of-sight ($Z= -2.481$, $p<0.05$).

The data for observations at Greater than Five Metres and Out-of-Sight are presented in a somewhat scaled-down form. This is partially due to the fact that such scans are relatively rare, and especially so for those individual cats seen at closer proximities (those more relevant in terms of the potential for interactions). Also, little additional information is encoded in these "unavailable" scans, and so they are only useful for analysis at the colony and individual levels (not for insight into dyadic interactions). Therefore, these "unavailable" categories are presented only for the initial investigation of spatial patterns (Section 3.2), and then again for comparisons of individual cats and their spacing from others (Section 3.4).

Spearman Correlations were performed to look for associations between different proximity scores for individuals; these results (Table 3.1.c) demonstrated strong positive linear relations between the two closer values and between the two further ones.

Table 3.1.a: Proximity Differences Between Cat Groups (n= 6 in Group A, 7 in Group B). There were no significant differences between the groups for any distance category, using totals for each individual cat in Mann-Whitney U-tests.

Proximity	**U**	**Z**	**p**
Contact	21	0	1
Less than Thirty Centimetres	12	-1.286	.199
Thirty Centimetres-One Metre	20	- .143	.886
One-Five Metres	20	- .143	.886
Total to Five Metres	19	- .286	.775
> Five Metres	15	- .862	.389
Out-of-Sight	17	- .571	.568
Total Unavailable	20.5	- .072	.943

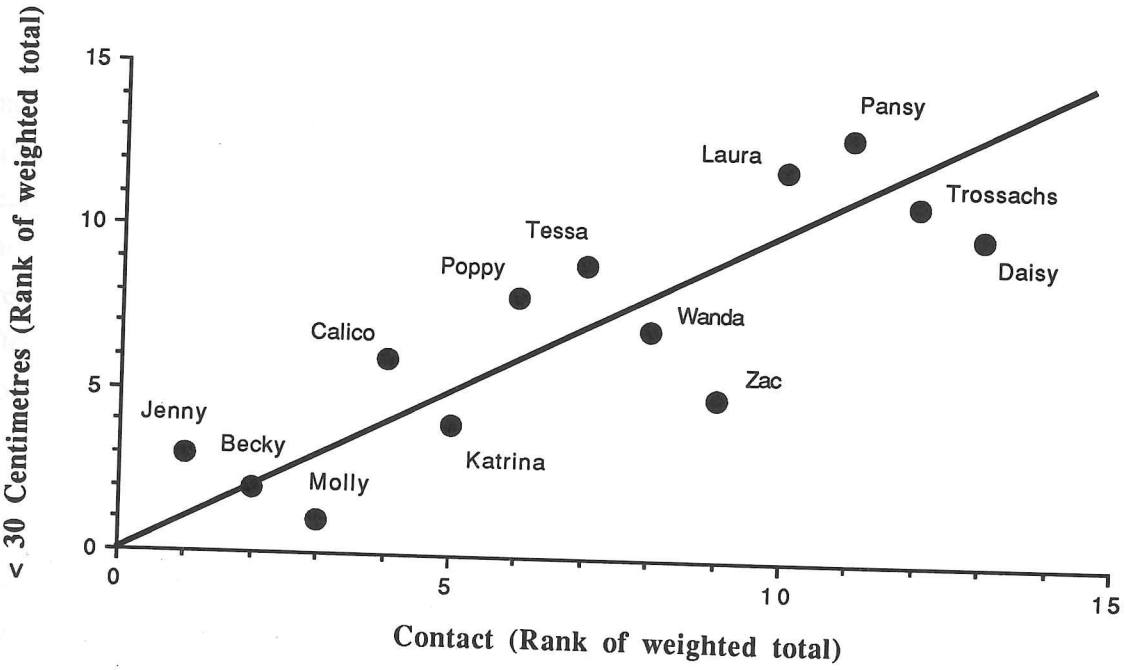
Table 3.1.b: Proximity Differences Between Cat Sexes (n= 2 Males, 11 Females). The only significant result, using a Mann-Whitney U-test, was for the One-Five Metres category, in which Male cats ranked higher than Females. Other strong trends are also indicated.

Proximity	**U**	**Z**	**p**		
Contact	3	-1.579	.114		(F>M)
Less than Thirty Centimetres	4	-1.382	.167		(F>M)
Thirty Centimetres-One Metre	9	- .395	.693		
One-Five Metres	1	-1.974	<0.05	*	(M>F)
Total to Five Metres	8	- .592	.554		
> Five Metres	10	- .198	.843		
Out-of-Sight	11	0	1		
Total Unavailable	9	- .395	.693		

Table 3.1.c: Spearman Correlations for All Individual Proximity Scores (n=13). Significant probability levels mean that the two variables tested have a linear relationship for the ranks of individual cats. An explanatory example is provided on the following page. Note that, due to the large number of variables tested together, significant values should be taken as indicative and not absolute.

Proximity 1	**Proximity 2**	r_s	Z	p	
Contact	Less than Thirty Centimetres	.659	2.284	<0.05	*
Contact	Thirty Centimetres-One Metre	.302	1.047	.295	
Contact	One-Five Metres	-.082	- .286	.775	
Contact	Total to Five Metres	.346	1.199	.231	
Contact	> Five Metres	-.635	-2.201	<0.05	*
Contact	Out-of-Sight	-.473	-1.637	.102	
Contact	Total Unavailable	-.619	-2.144	<0.05	*
Less than Thirty Centimetres	Thirty Centimetres-One Metre	.489	1.694	.090	
Less than Thirty Centimetres	One-Five Metres	.093	.324	.746	
Less than Thirty Centimetres	Total to Five Metres	.516	1.789	.074	
Less than Thirty Centimetres	> Five Metres	-.619	-2.144	<0.05	*
Less than Thirty Centimetres	Out-of-Sight	-.720	-2.493	<0.05	*
Less than Thirty Centimetres	Total Unavailable	-.784	-2.716	<0.01	**
Thirty Centimetres-One Metre	One-Five Metres	.846	2.931	<0.01	**
Thirty Centimetres-One Metre	Total to Five Metres	.973	3.369	<0.001	***
Thirty Centimetres-One Metre	> Five Metres	-.669	-2.316	<0.05	*
Thirty Centimetres-One Metre	Out-of-Sight	-.764	-2.646	<0.01	**
Thirty Centimetres-One Metre	Total Unavailable	-.765	-2.649	<0.01	**
One-Five Metres	Total to Five Metres	.841	2.912	<0.01	**
One-Five Metres	> Five Metres	-.453	-1.569	.117	
One-Five Metres	Out-of-Sight	-.549	-1.903	.057	
One-Five Metres	Total Unavailable	-.501	-1.734	.083	
Total to Five Metres	> Five Metres	-.713	-2.469	<0.05	*
Total to Five Metres	Out-of-Sight	-.791	-2.741	<0.01	**
Total to Five Metres	Total Unavailable	-.823	-2.849	<0.01	**
> Five Metres	Out-of-Sight	.646	2.239	<0.05	*
> Five Metres	Total Unavailable	.869	3.009	<0.01	**
Out-of-Sight	Total Unavailable	.916	3.173	<0.01	**

Supplement to Table 3.1.c: An example scattergram, using hypothetical values, to explain the Spearman Correlation style of analysis used in Chapter 3 (and again in Chapter 4). The correlation is performed using each individual Adult as a point, therefore n=13, with ranked scores. The x-axis (abscissa) is the rank of the weighted total for Contact (for each individual cat), and the y-axis (ordinate) is the rank of the weighted total for observations at Less than 30 Centimetres. Each point (cat) has a particular combination of Contact and Less than 30 Centimetres scores, which were found across all possible partners, and these are first converted to ranks relative to all the other individuals. A Spearman Correlation then looks for a linear relationship between the sets of ranks. Here, the correlation coefficient (r_s) is positive, indicating that, as the relative rank for Contact totals increases, the relative rank for Less than 30 Centimetres increases in a linear manner. In other words, Contact and Less than 30 Centimetres have linearly related ranks; a cat with a low Contact score tends to have a low score for Less than 30 Centimetres, while a high Contact cat has a high total for Less than 30 Centimetres. From a relationship such as the one shown, it is possible to see that individual cats have consistent spatial patterns when comparing Contact and Less than 30 Centimetres for proximity relationships.



These associations allowed the possibility of lumping the data where general trends were explored, rather than (or as a supplement to) the more exact details; therefore, Contact was pooled with Less than Thirty Centimetres, hence called "NEAR", and Thirty Centimetres to One Metre and One to Five Metres were similarly combined to create a "FAR" value.

Female-Female associations made up the vast majority of possible combinations, especially when younger Females were also included; Adult Female-Adult Female proximity dyads were more frequent than any other pairing at all distances (Figure 3.1), followed by Adult Female-Juvenile Female and Adult Female-Juvenile Male. The details of specific partners and individual differences are discussed in later sections.

3.2.2. FEMALE-MALE RELATIONSHIPS

Female-Male proximity relationships were skewed somewhat by the fact that, for the greatest part of the study, Males could only interact with Adult Females, Juveniles or Kittens; due to a marked intolerance for younger cats, Males spent more time near Adult Females. Adult Females, on the other hand, were more tolerant of young cats and had the choice of Male or Female proximity partners. Both Trossachs and Zac had a preferred partner, which depended somewhat on the distance category; the cat found most often in Contact was not the same as that found "near", due to the relative infrequency of Contact.

Females spent relatively large amounts of scanned time in the environs of Males, who often ranked second or third of all possible associates. Most of the score developed from the long-range relations, but, for some Females, close affiliations were also present (e.g. Katrina, Jenny, Calico, Wanda, Laura and Molly). Adult Female-Adult Male scores, across the whole colony, were lower than with Juvenile Males, but followed a similar pattern, increasing from closer distances to farther ones. Differences are shown graphically in Figures 3.1.a and b, with summarising transition matrices in Figures 3.1.c and d.

3.2.3. MALE-MALE RELATIONSHIPS

Examination of Male-Male proximity was constrained by the fact that each group was founded by a single Adult Male. However, by 1989, Male offspring had become Adult, and it is to these interactions that the section refers. Adult Males were almost never found in Contact with their Adult sons, especially when compared to levels with Females; they also spent very few scans at Less than Thirty Centimetres and Thirty Centimetres to One Metre. Scores for One to Five Metres were somewhat less depressed, but were still generally lower than for other possible associates. Over all distances, Adult Males were found least with other Males, with the possible exception of Zac and his sons,

Figure 3.1.a

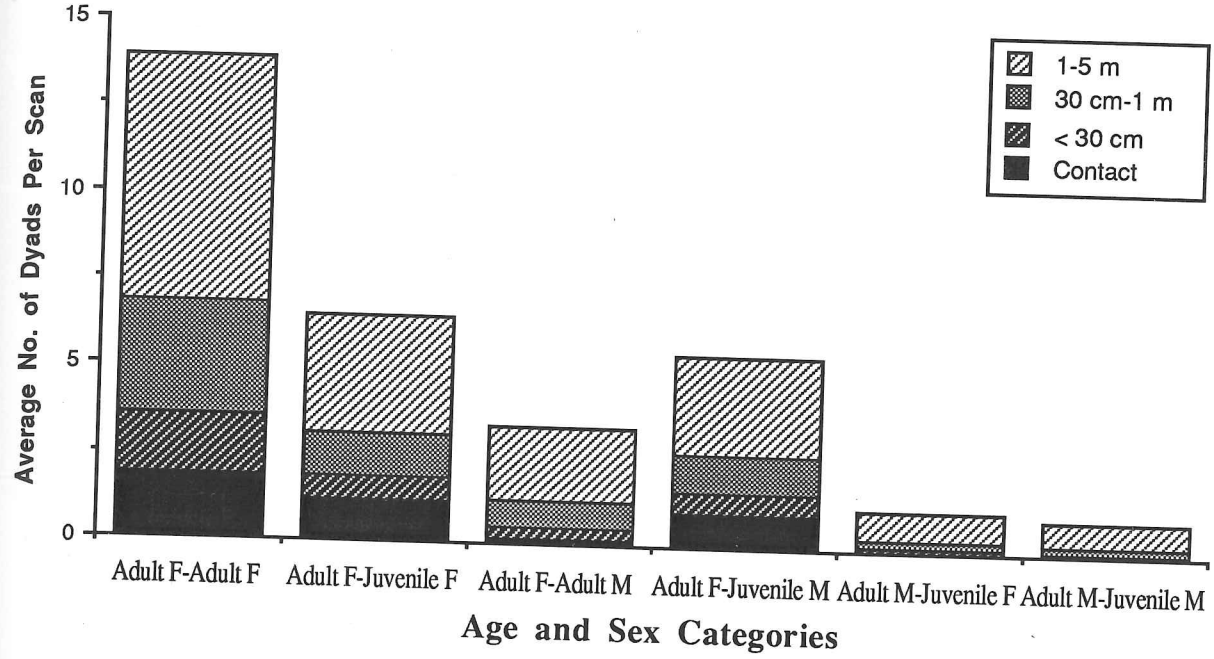


Figure 3.1.b

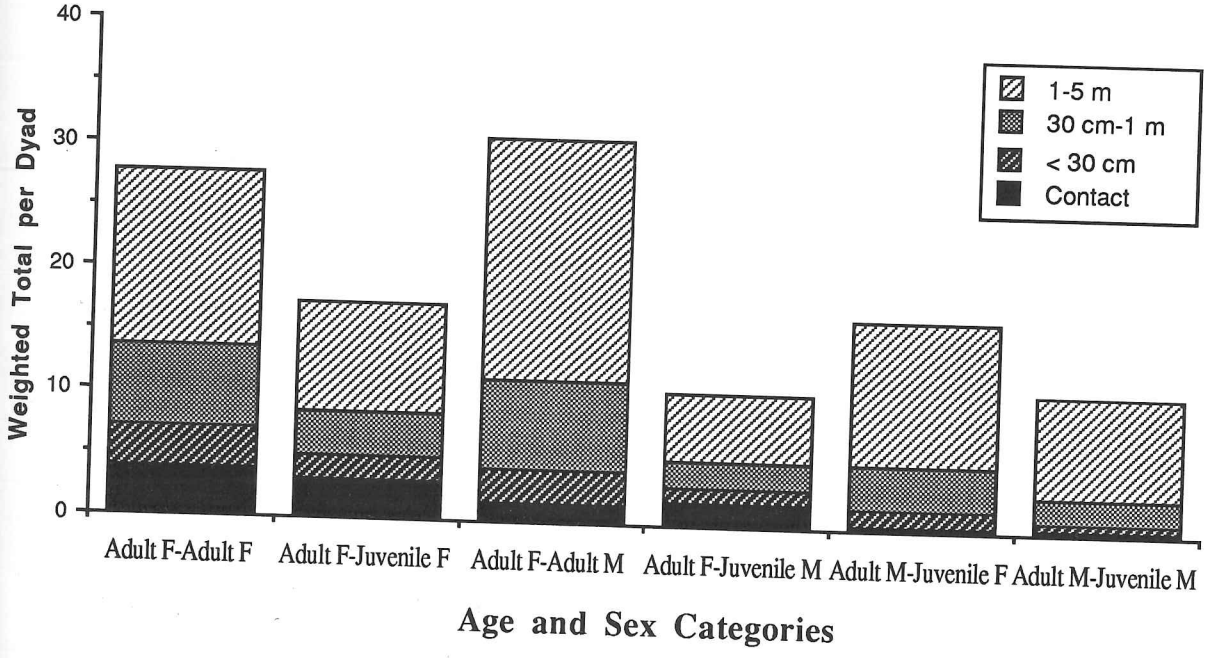


Figure 3.1: Colony totals for proximity distances. Each column represents different age and sex class categories and their associations. (a) The colony total given as the average number of dyadic combinations per scan; (b) Totals are given as the weighted total per dyad for each age and sex class combination.

Figure 3.1.c

Contact / < 30 cm	Trossachs	Katrina	Becky	Tessa	Pansy	Poppy
Trossachs		1.085	0.164	0.327	0.327	0.327
Katrina	3.037		1.302	0.868	2.386	9.978
Becky	1.637	1.302		15.710	1.637	5.401
Tessa	2.128	2.820	6.547		0.164	5.728
Pansy	1.309	3.254	2.455	2.619		1.800
Poppy	4.092	6.291	4.910	7.365	4.910	

Contact / < 30 cm	Zac	Jenny	Calico	Wanda	Laura	Molly	Daisy
Zac		3.764	3.110	4.255	1.736	1.309	0.327
Jenny	4.910		4.746	6.710	5.556	6.056	0.655
Calico	2.782	4.583		8.838	4.514	0.982	0
Wanda	3.437	5.401	6.219		2.083	1.800	0.327
Laura	2.431	2.951	1.736	1.563		6.944	0
Molly	2.946	4.419	1.309	3.110	3.993		0
Daisy	1.473	2.455	0.491	1.309	0.694	0.655	

Figure 3.1.c: Transition matrices giving the corrected proximity data for each individual Adult at the two closer distances. The upper matrix is Group A, the lower matrix is Group B, and the Adult Male is given as the first name. In each matrix, the top right half summarises the Contact data, while the lower left half is the data for Less than 30 Centimetres.

Figure 3.1.d

30 cm-1 m 1-5 m	Trossachs	Katrina	Becky	Tessa	Pansy	Poppy
Trossachs		7.375	5.074	9.329	4.583	6.056
Katrina	16.486		5.640	6.291	3.254	6.725
Becky	19.804	12.798		10.966	5.892	8.347
Tessa	19.640	16.269	16.694		4.255	9.656
Pansy	12.602	4.772	10.966	13.584		3.928
Poppy	16.039	11.714	13.912	17.021	9.820	

30 cm-1 m 1-5 m	Zac	Jenny	Calico	Wanda	Laura	Molly	Daisy
Zac		11.784	7.038	8.183	8.160	7.038	3.764
Jenny	27.496		6.056	10.802	9.375	13.421	6.383
Calico	15.057	15.385		6.383	4.688	3.928	2.619
Wanda	22.259	21.277	11.129		5.729	6.219	4.910
Laura	21.354	17.708	9.375	12.674		7.986	3.646
Molly	25.368	20.949	13.421	17.021	16.667		6.547
Daisy	16.694	17.676	10.638	15.221	13.194	12.766	

Figure 3.1.d: Transition matrices giving the corrected proximity data for each individual Adult at the two farther distances. The upper matrix is Group A, the lower matrix is Group B, and the Adult Male is given as the first name. In each matrix, the top right half summarises the data for 30 Centimetres to 1 Metre, while the lower left half is the data for 1 to 5 Metres.

Carbonel and Dijon, who appeared to maintain a higher profile in the core area without exciting the agonistic attentions of the Adult Male. However, even in this case, the inter-Male values were low, although not as low as with certain more solitary Females (e.g. Daisy).

As mentioned, it was generally impossible to scan the proximities of Juveniles as Focal animals, primarily due to the more secluded nature of their active areas; therefore inter-Male spatial relations were not quantifiable for Juveniles. A tendency was noticed for these Males to remain in a group together, often venturing into the core area together, and even resting in a common hut or other sleeping place. As the Males grew older, this type of "coalition" became less evident, especially for the two larger Males (Dijon and Doolittle); Catkin and Carbonel seemed to incur less agonism from Adults and, around this time, began to hover around the central food area and the Adult Females. In some ways, they behaved almost as if not Male, or at least not mature, despite starting to spray-mark and mount. These behavioural aspects are discussed at length in Chapter 4.

3.2.4. ADULT-JUVENILE RELATIONSHIPS

Adult Females spent more scans with Juvenile Females than Juvenile Males at all distances; of these, a larger portion were with 1987 individuals, except for Contact (Figures 3.2.a & b). Adult Males were more often around Juvenile Females, and particularly with those cats born in 1987.

The total proximity scores for Adults to all Juveniles are shown in Figure 3.2.c. Females typically had higher scores at closer distances, although not all Females were high-ranked for Contact itself (e.g. Pippin); this was true for both Groups A and B. Individuals varied quite a lot, from a weighted total of 45 (Doolittle) to 184 (Mulberry); this mainly reflected differences in availability due to spatial relationships with Adults. The Juveniles who had more affiliative interactions with Adults were more often within five metres of them, while the Juveniles who lacked these social relationships were often out-of-sight and away from the core area.

The two groups showed differences in their proximity to the Juvenile Males and Females, due to the unequal distribution between the sides. Group A had three Juvenile Females and one Male from 1987, and an additional two Females and one Male from 1988; Group B was the opposite, with one Female and four Males from 1987, plus one Female and three Males from 1988. The discrepancy in the sex-ratio of surviving young cats resulted in diverse relationships between the groups, which were approached by pooling all Juveniles for a broader perspective. Most Group A Females were near some Juveniles only, but Poppy showed a more general interest, although less marked for the Males. The Adult Male echoed the Females' preferences. Group B Females were similar,

Figure 3.2.a

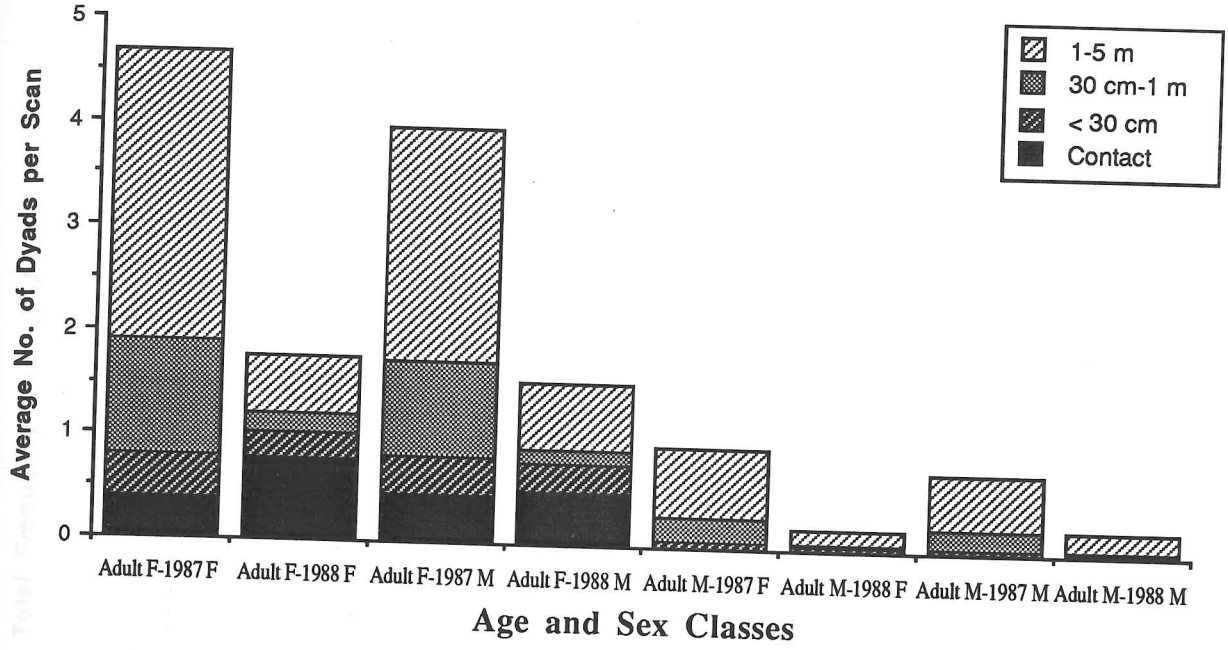


Figure 3.2.b

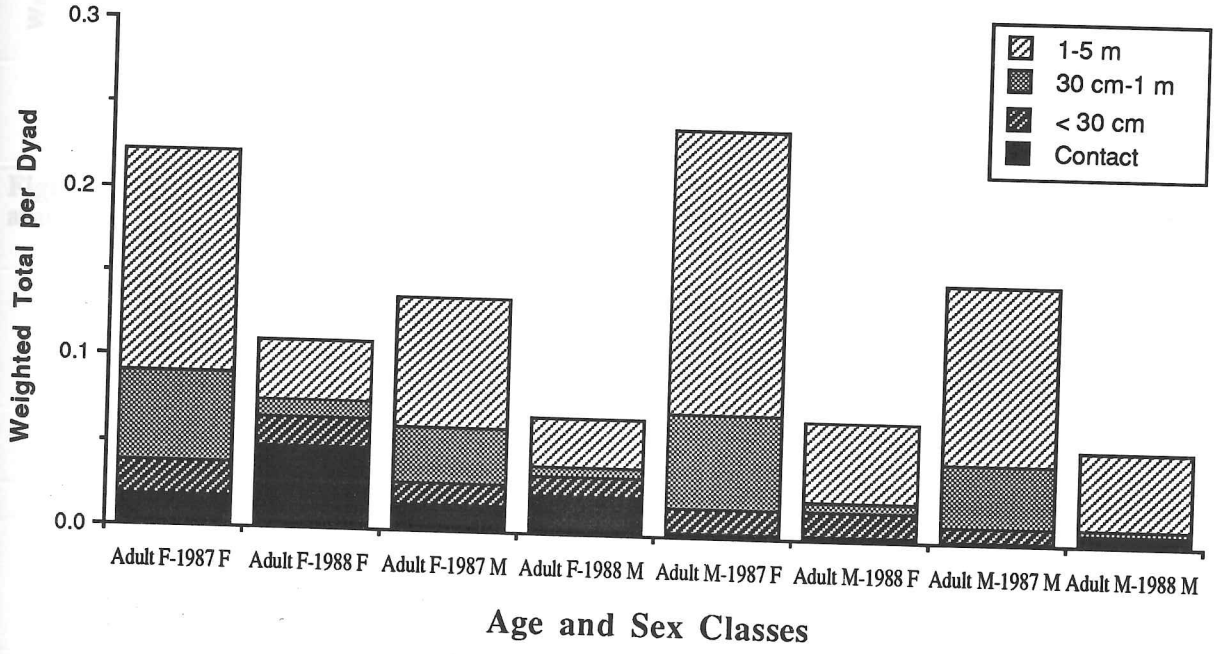


Figure 3.2: Adult proximity to Juveniles, both Males and Females, from 1987 and 1988. (a) Data are given as the average number of each dyadic combination seen per observation scan; (b) Weighted total per dyad for each age and sex class combination.

Figure 3.2.c

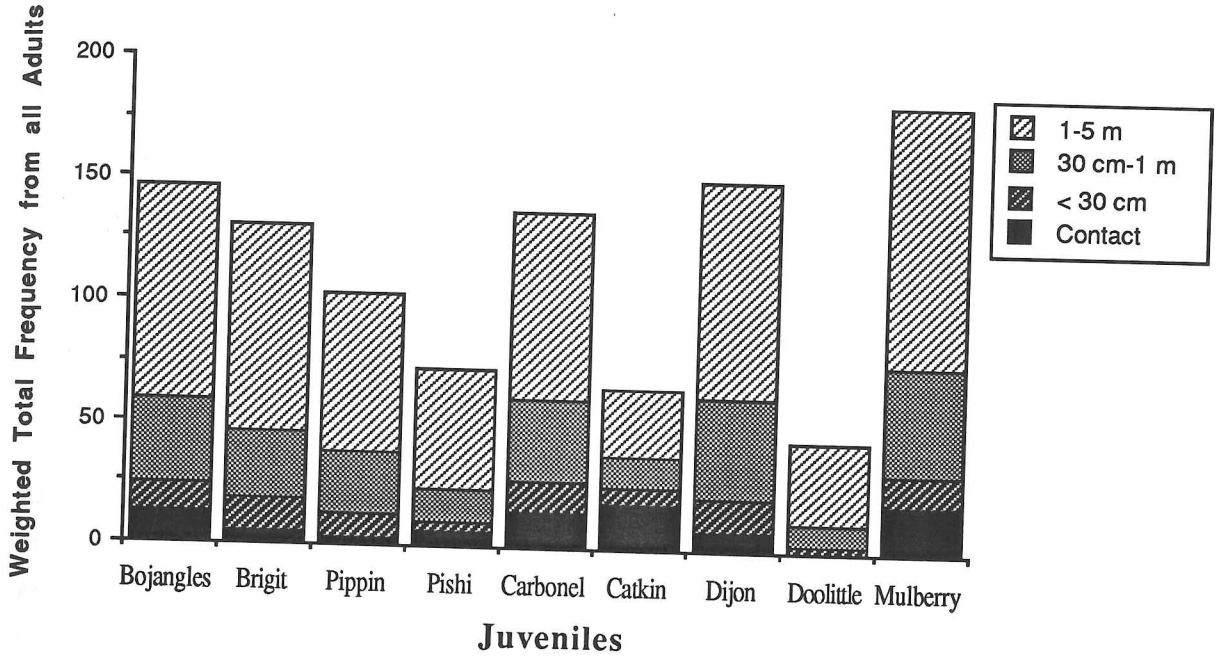


Figure 3.2.c: Juvenile proximity to Adults for individuals born in 1987, weighted by Adult availability.

in that most preferred the Juvenile Female (Mulberry), as did the Adult Male; however, both Calico and Daisy, Females with surviving offspring, were found more with their own sons (e.g. Carbonel, Catkin and Dijon). Other individual differences are explored later in the chapter (Section 3.4).

3.2.5. JUVENILE-JUVENILE RELATIONSHIPS

There was very little information on the spatial relationships between Juvenile cats, as they were never the Focal subjects for proximity scans. In general, young cats seemed to remain together, often separate from other individuals in the group. Through the winter of 1987, Juveniles on Side A were rarely seen, due to the group inhabitation of a large woodpile and their apparent timidity; even when Adult, these individuals were often found together. A similar tendency was seen in the Juveniles, mainly Male, on Side B.

These younger cats also appeared to take notice of peers in the adjoining group, although inter-group associations were not analysed due to their relative rarity among Focal Adults. Cross-fence encounters were mixed, and included both Male-Male and Male-Female combinations. Male-Male interactions were often investigative and seldom prolonged, occasionally involving sniffing and rubbing, usually initiated by mutual approach; a few scans included an Adult plus a Juvenile, often watching or sniffing at one another. Young Males were seen to roll on the ground in the presence of Adult Males upon occasion, as will be discussed within groups in Chapter 4. Male-Female encounters were similarly casual, and seldom included Adult Females; Males took some interest in the maturing Females of the other group, especially Pishi with Mulberry, but again, close proximity was brief and often non-interactive.

3.2.6. KITTEN RELATIONSHIPS

As already mentioned, Kittens were considered at two different levels: when they were a cohesive young litter (in terms of Female's preferences for own or other litters, described in Section 3.4.4); and when they were more independent individuals, and technically young Juveniles. The latter case is examined in this section, along with some overall aspects affecting scores for young cats.

Proximity measures for Kittens were found from the scans of Focal Adults, and represent summed values over all Adults. These scores are shown in Figure 3.3.a, only for those Kittens that remained from birth throughout the rest of the study (n=7). As with the totals for Juveniles, a lot of variation was evident, from a weighted total of 26 (Dickory) to 92 (Tycho).

Figure 3.3.a

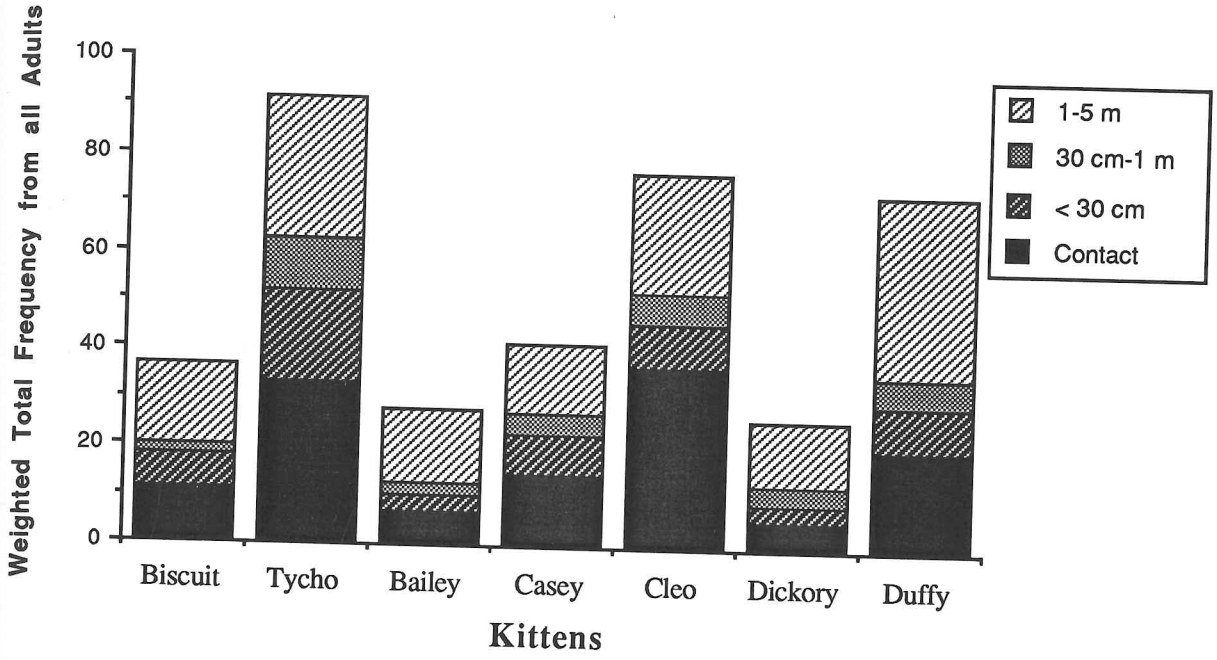


Figure 3.3.a: Kitten proximity to Adults, for those individuals born in 1988. Values are weighted by Adult availability. Group A individuals are presented first (on the left) and then Group B Kittens are listed.

Figure 3.3.b

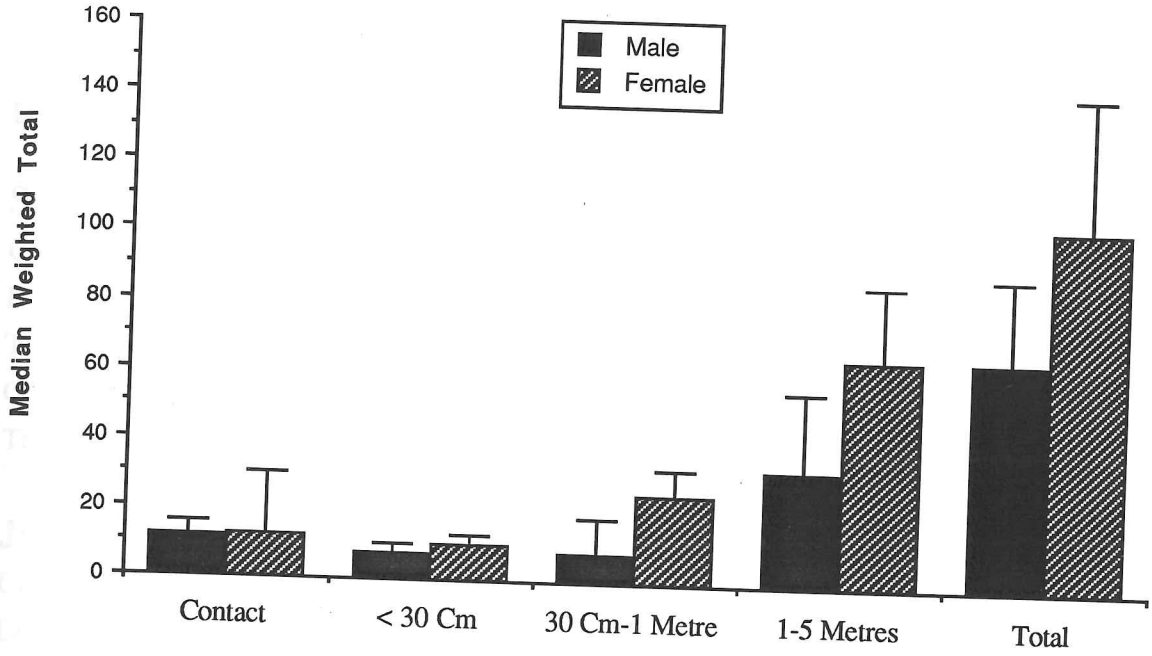


Figure 3.3.c

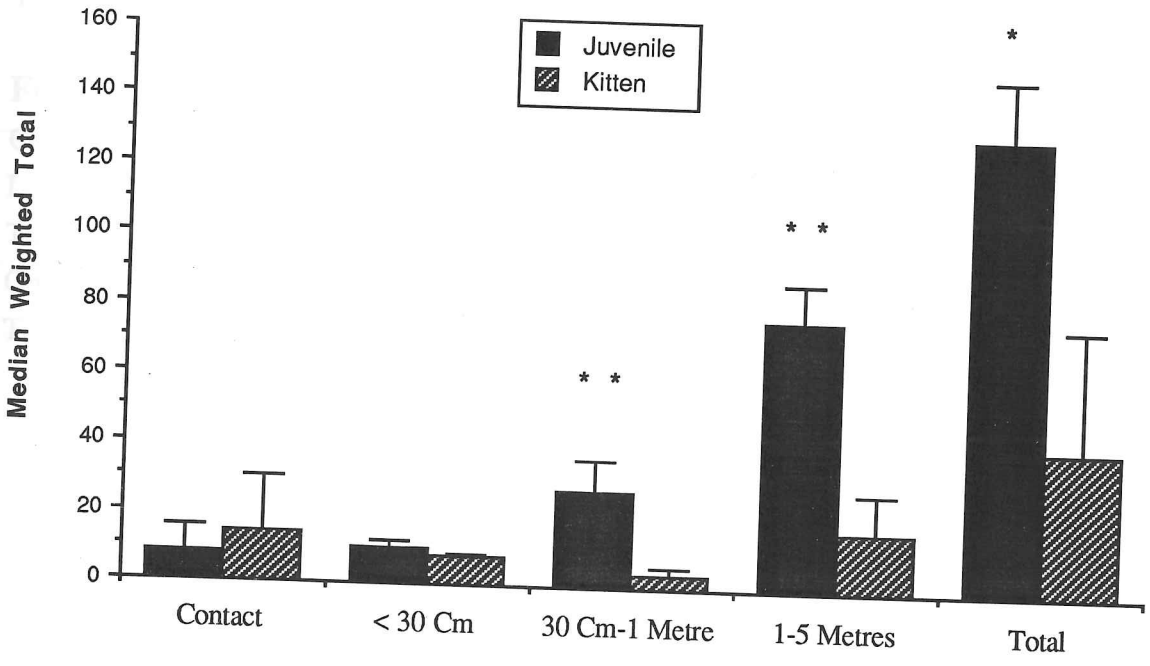


Figure 3.3: Differences in the proximity scores from Adults for Juveniles and Kittens. Medians and interquartile ranges are shown. (**b**) Sex Class Differences; (**c**) Age Class Differences. *p<0.05, **p<0.01 (Mann-Whitney U-tests)

Table 3.2: Proximity Values for Juveniles and Kittens. Significant probability levels indicate differences for the tested variables, e.g. Juveniles have higher ranked scores than Kittens at One to Five Metres, using a Mann-Whitney U-test.

Distance	n	U	Z	p		
Side A vs. B						
Contact	7,9	20	-1.217	.224		
Less than Thirty Centimetres	7,9	24	- .794	.427		
Thirty Centimetres to One Metre	7,9	30	- .159	.874		
One to Five Metres	7,9	29	- .265	.791		
Total to Five Metres	7,9	31	- .053	.958		
Juvenile vs. Kitten						
Contact	9,7	17	-1.535	.125		
Less than Thirty Centimetres	9,7	29	- .265	.791		
Thirty Centimetres to One Metre	9,7	1	-3.228	<0.01	**	(J>K)
One to Five Metres	9,7	3	-3.017	<0.01	**	(J>K)
Total to Five Metres	9,7	9	-2.382	<0.05	*	(J>K)
Female vs. Male						
Contact	7,9	27	- .476	.634		
Less than Thirty Centimetres	7,9	24	- .794	.427		
Thirty Centimetres to One Metre	7,9	22	-1.006	.315		
One to Five Metres	7,9	22	-1.006	.315		
Total to Five Metres	7,9	17	-1.535	.125		

Juvenile and Kitten values were combined in order to test certain factors such as group, age and sex (each age category was too small alone to allow meaningful statistics); in fact, when sampled, the so-called Kittens were technically Juveniles and were kept separate only for the purposes of distinguishing them from the Juveniles born in 1987 who were present during all of the study. Group identity did not influence the proximity scores of Juveniles and Kittens, nor did sex class; however, the difference between Kittens and Juveniles was significant (Table 3.2), such that Juveniles had higher scores for the longer distances. The median values for the two sexes are plotted in Figure 3.3.b, and the values for Juveniles versus Kittens in Figure 3.3.c.

When a correlation analysis was run across all distances, only Thirty Centimetres to One Metre was associated with One to Five Metres (r_S= .929, Z= 3.600, $p<0.001$, n= 16), such that individuals sampled often at medium distances were also sampled more frequently at further distances.

3.3. THE DYAD

3.3.1. FEMALE-FEMALE

A total of 87 dyads involved two Females; these all included a Focal Adult as explained in Section 3.1.2. Of the dyads, 50 were Adult-Adult, and the remaining 37 were Adult-Juvenile (although 21 of these became Adult-Adult during the course of the study).

Each Adult was tested across all dyad partners for correlations between proximities (e.g. consistencies with the same partner at different distances); individuals varied as to the set of distance relationships that were seen (Table 3.3.a). Males were consistent between most distances in terms of their specific partners; Group A Females were mainly correlated for the two farther proximities; and Group B Females varied from individuals like Jenny and Molly, who had related scores at all distances, to Calico, who was consistent only at close proximity. It is likely that this breadth of patterns related to specific dyadic relationships and was characteristic to specific individuals.

The next analysis then considered individual preferences for certain age or sex classes in dyadic proximity relationships; Females generally displayed no differences in proximity patterns with either sex of interactant, except for Calico at One to Five Metres (who preferred Females: U= 11, Z= -1.967, $p<0.05$, n= 8,7) and Molly at Thirty Centimetres to One Metre (who also preferred Females : U= 10.5, Z= -2.031, $p<0.05$, n= 8,7). Age classes did show greater differences (Table 3.3.b), such that Adults ranked over Juveniles and Kittens as partners at most distances; this was true for Females and

Table 3.3.a: Individual Correlations Across Dyad Partners (n=12 for Group A and n=15 for Group B). Each cat is tested at different distances from all potential partners. Significant probability levels mean that the two variables tested have a linear relationship for the ranks of individual partners, e.g. the ranks of proximity for Katrina with all other cats are significantly linearly correlated between the distance categories 30 cm-1 m versus 1-5 m. In practice, this means that the same individual cats are often seen at 30 cm-1 m and 1-5 m from Katrina (and similarly for those rarely seen). Note that, due to the large number of variables tested together, significance levels should be taken as indicative and not absolute. Note however that some cats show significant correlations over all distances (compared with the few correlations for most other cats), clearly indicating spatial relationships that are more consistent over all distances.

Group	Name	Distances	r_s	Z	p	
FEMALES						
A	Katrina	C - < 30cm	.251	.834	.405	
A	Katrina	C - 30cm-1m	-.355	-1.177	.239	
A	Katrina	C - 1-5m	-.583	-1.935	.053	
A	Katrina	< 30cm - 30cm-1m	.425	1.408	.159	
A	Katrina	< 30cm - 1-5m	.196	.652	.515	
A	Katrina	30cm-1m - 1-5m	.916	3.037	<0.01	**
A	Becky	C - < 30cm	.801	2.658	<0.01	**
A	Becky	C - 30cm-1m	.533	1.769	.077	
A	Becky	C - 1-5m	.186	.617	.537	
A	Becky	< 30cm - 30cm-1m	.708	2.347	<0.05	*
A	Becky	< 30cm - 1-5m	.567	1.882	.060	
A	Becky	30cm-1m - 1-5m	.734	2.435	<0.05	*
A	Tessa	C - < 30cm	.575	1.909	.056	
A	Tessa	C - 30cm-1m	.095	.314	.753	
A	Tessa	C - 1-5m	-.109	- .361	.718	
A	Tessa	< 30cm - 30cm-1m	.580	1.925	.054	
A	Tessa	< 30cm - 1-5m	.469	1.554	.120	
A	Tessa	30cm-1m - 1-5m	.916	3.038	<0.01	**
A	Pansy	C - < 30cm	.572	1.896	.058	
A	Pansy	C - 30cm-1m	.435	1.442	.149	
A	Pansy	C - 1-5m	.186	.616	.538	
A	Pansy	< 30cm - 30cm-1m	.578	1.917	.055	
A	Pansy	< 30cm - 1-5m	.607	2.013	<0.05	*
A	Pansy	30cm-1m - 1-5m	.851	2.823	<0.01	**
A	Poppy	C - < 30cm	.567	1.882	.060	
A	Poppy	C - 30cm-1m	.252	.835	.404	
A	Poppy	C - 1-5m	-.056	- .186	.853	
A	Poppy	< 30cm - 30cm-1m	.732	2.428	<0.05	*
A	Poppy	< 30cm - 1-5m	.462	1.533	.125	
A	Poppy	30cm-1m - 1-5m	.804	2.667	<0.01	**
B	Jenny	C - < 30cm	.732	2.739	<0.01	**
B	Jenny	C - 30cm-1m	.656	2.454	<0.05	*
B	Jenny	C - 1-5m	.554	2.071	<0.05	*
B	Jenny	< 30cm - 30cm-1m	.838	3.136	<0.01	**
B	Jenny	< 30cm - 1-5m	.754	2.820	<0.01	**
B	Jenny	30cm-1m - 1-5m	.879	3.290	<0.001	***

Group	Name	Distances	r_s	Z	p	
B	Calico	C - < 30cm	.782	2.927	<0.01	**
B	Calico	C - 30cm-1m	-.070	- .261	.794	
B	Calico	C - 1-5m	-.286	-1.069	.285	
B	Calico	< 30cm - 30cm-1m	.281	1.050	.294	
B	Calico	< 30cm - 1-5m	.146	.548	.584	
B	Calico	30cm-1m - 1-5m	.878	3.284	<0.001	***
B	Wanda	C - < 30cm	.769	2.877	<0.01	**
B	Wanda	C - 30cm-1m	.501	1.876	.061	
B	Wanda	C - 1-5m	.338	1.263	.207	
B	Wanda	< 30cm - 30cm-1m	.629	2.355	<0.05	*
B	Wanda	< 30cm - 1-5m	.456	1.705	.088	
B	Wanda	30cm-1m - 1-5m	.858	3.210	<0.01	**
B	Laura	C - < 30cm	.700	2.618	<0.01	**
B	Laura	C - 30cm-1m	.621	2.322	<0.05	*
B	Laura	C - 1-5m	.377	1.409	.159	
B	Laura	< 30cm - 30cm-1m	.902	3.374	<0.001	***
B	Laura	< 30cm - 1-5m	.824	3.082	<0.01	**
B	Laura	30cm-1m - 1-5m	.918	3.436	<0.001	***
B	Molly	C - < 30cm	.798	2.985	<0.01	**
B	Molly	C - 30cm-1m	.688	2.573	<0.05	*
B	Molly	C - 1-5m	.772	2.889	<0.01	**
B	Molly	< 30cm - 30cm-1m	.770	2.880	<0.01	**
B	Molly	< 30cm - 1-5m	.851	3.183	<0.01	**
B	Molly	30cm-1m - 1-5m	.881	3.296	<0.001	***
B	Daisy	C - < 30cm	.300	1.123	.261	
B	Daisy	C - 30cm-1m	.104	.391	.696	
B	Daisy	C - 1-5m	.409	1.531	.126	
B	Daisy	< 30cm - 30cm-1m	.831	3.110	<0.01	**
B	Daisy	< 30cm - 1-5m	.876	3.279	<0.001	***
B	Daisy	30cm-1m - 1-5m	.847	3.169	<0.01	**

MALES

A	Trossachs	C - < 30cm	.694	2.302	<0.05	*
A	Trossachs	C - 30cm-1m	.857	2.844	<0.01	**
A	Trossachs	C - 1-5m	.713	2.366	<0.05	*
A	Trossachs	< 30cm - 30cm-1m	.795	2.637	<0.01	**
A	Trossachs	< 30cm - 1-5m	.585	1.940	.052	
A	Trossachs	30cm-1m - 1-5m	.888	2.946	<0.01	**
B	Zac	C - < 30cm	.792	2.965	<0.01	**
B	Zac	C - 30cm-1m	.672	2.515	<0.05	*
B	Zac	C - 1-5m	.573	2.143	<0.05	*
B	Zac	< 30cm - 30cm-1m	.872	3.262	<0.01	**
B	Zac	< 30cm - 1-5m	.799	2.991	<0.01	**
B	Zac	30cm-1m - 1-5m	.894	3.346	<0.001	***

N.B. "C" represents the measure of Contact, while other distances are given using the abbreviations for centimetres and metres.

Table 3.3.b: Differences in Age Class of Proximity Partners, Using a Kruskal-Wallis Test. A significant result means that the three age classes were ranked differently at that distance. (Usually Adult > Juvenile > Kitten)

Group	Name	Distance	df	n	H	p	
FEMALES							
A	Katrina	Contact	2	12	2.660	.265	
A	Katrina	< 30cm	2	12	2.500	.287	
A	Katrina	30cm-1m	2	12	7.955	<0.05	*
A	Katrina	1-5m	2	12	6.565	<0.05	*
A	Katrina	Total to 5m	2	12	6.410	<0.05	*
A	Becky	Contact	2	12	3.009	.222	
A	Becky	< 30cm	2	12	4.136	.126	
A	Becky	30cm-1m	2	12	8.446	<0.05	*
A	Becky	1-5m	2	12	6.785	<0.05	*
A	Becky	Total to 5m	2	12	7.876	<0.05	*
A	Tessa	Contact	2	12	3.438	.179	
A	Tessa	< 30cm	2	12	2.953	.229	
A	Tessa	30cm-1m	2	12	7.477	<0.05	*
A	Tessa	1-5m	2	12	6.785	<0.05	*
A	Tessa	Total to 5m	2	12	5.804	.055	
A	Pansy	Contact	2	12	5.488	.064	
A	Pansy	< 30cm	2	12	8.207	<0.05	*
A	Pansy	30cm-1m	2	12	7.927	<0.05	*
A	Pansy	1-5m	2	12	7.121	<0.05	*
A	Pansy	Total to 5m	2	12	8.446	<0.05	*
A	Poppy	Contact	2	12	2.522	.283	
A	Poppy	< 30cm	2	12	5.587	.061	
A	Poppy	30cm-1m	2	12	5.814	.055	
A	Poppy	1-5m	2	12	6.369	<0.05	*
A	Poppy	Total to 5m	2	12	4.060	.131	
B	Jenny	Contact	2	15	5.021	.081	
B	Jenny	< 30cm	2	15	9.081	<0.05	*
B	Jenny	30cm-1m	2	15	9.752	<0.01	**
B	Jenny	1-5m	2	15	8.228	<0.05	*
B	Jenny	Total to 5m	2	15	9.562	<0.01	**

Group	Name	Distance	df	n	H	p	
B	Calico	Contact	2	15	3.348	.188	
B	Calico	< 30cm	2	15	1.688	.430	
B	Calico	30cm-1m	2	15	8.724	<0.05	*
B	Calico	1-5m	2	15	9.081	<0.05	*
B	Calico	Total to 5m	2	15	3.336	.189	
B	Wanda	Contact	2	15	5.152	.076	
B	Wanda	< 30cm	2	15	4.314	.116	
B	Wanda	30cm-1m	2	15	10.909	<0.01	**
B	Wanda	1-5m	2	15	9.978	<0.01	**
B	Wanda	Total to 5m	2	15	9.748	<0.01	**
B	Laura	Contact	2	15	2.231	.328	
B	Laura	< 30cm	2	15	7.333	<0.05	*
B	Laura	30cm-1m	2	15	8.920	<0.05	*
B	Laura	1-5m	2	15	9.573	<0.01	**
B	Laura	Total to 5m	2	15	8.363	<0.05	*
B	Molly	Contact	2	15	3.127	.209	
B	Molly	< 30cm	2	15	4.826	.090	
B	Molly	30cm-1m	2	15	9.331	<0.01	**
B	Molly	1-5m	2	15	8.685	<0.05	*
B	Molly	Total to 5m	2	15	8.856	<0.05	*
B	Daisy	Contact	2	15	1.592	.451	
B	Daisy	< 30cm	2	15	8.599	<0.05	*
B	Daisy	30cm-1m	2	15	8.926	<0.05	*
B	Daisy	1-5m	2	15	10.900	<0.01	**
B	Daisy	Total to 5m	2	15	9.961	<0.01	**
MALES							
A	Trossachs	Contact	2	12	5.243	.073	
A	Trossachs	< 30cm	2	12	5.289	.071	
A	Trossachs	30cm-1m	2	12	7.096	<0.05	*
A	Trossachs	1-5m	2	12	6.785	<0.05	*
A	Trossachs	Total to 5m	2	12	7.096	<0.05	*
B	Zac	Contact	2	15	7.826	<0.05	*
B	Zac	< 30cm	2	15	9.053	<0.05	*
B	Zac	30cm-1m	2	15	10.929	<0.01	**
B	Zac	1-5m	2	15	9.742	<0.01	**
B	Zac	Total to 5m	2	15	10.223	<0.01	**

Males. When all cats were compared together, a slightly more refined picture emerged; all cats preferred Females at all distances (Contact: U= 1911, Z= -2.337, $p<0.05$; Less than Thirty Centimetres: U= 1252.5, Z= -5.054, $p<0.001$; Thirty Centimetres to One Metre: U= 1285, Z= -4.919, $p<0.001$; One to Five Metres: U= 1277.5, Z= -4.948, $p<0.001$; and Overall: U= 1164.5, Z= -5.415, $p<0.001$; all n= 66 Males, 75 Females). Juveniles were, in total, the preferred age class for all proximity distances, followed usually by Adults and then Kittens, except for Contact (Contact: H= 6.987, $p<0.05$; Less than Thirty Centimetres: H= 33.327, $p<0.001$; Thirty Centimetres to One Metre: H= 94.139, $p<0.001$; One to Five Metres: H= 87.904, $p<0.001$; and Overall: H= 69.611, $p<0.001$; all df= 2, n= 141).

When "preferred" proximity partners were examined for Near (contact and up to thirty centimetres) and Far (thirty centimetres to five metres) distances, Females tended to be found, at close distances, with Females who were Communal partners or helpers; this was not true at greater distances (except for Becky with Tessa) or for total distance measures. All favoured partners are shown schematically (in Figures 3.4.a & b) for the two most extreme cases, Contact and the Total to Five Metres. Contact represents a closer distance and, presumably, a closer relationship; the Total to Five Metres may illustrate core members (e.g. net recipients) and more general sets of relationships. An interesting trend shown was the tendency, over the eighteen months of data collection, for Females who cooperated at some time to be found together as "preferred" partners (e.g. Poppy and Katrina, Tessa and Becky, Calico and Wanda, Molly and Laura).

3.3.2. FEMALE-MALE

Female-Male dyads numbered 63 in total, 11 of which were with Adult males, 52 with Juveniles (29 of these dyads became Adult during the study). Females were found at all distances from Males, from Contact to greater than five metres; the relative scarcity of Males allowed fewer possibilities than with other Females. Overall, Males were fairly highly ranked among a Female's dyadic partners, but this was often a result of frequent sightings of the pair within the same five metre radius. Individual Females differed as to the Male preferred, from the resident Adult to various Juveniles; in Group A, all Adult Females spent more scans in Contact with the younger Male, Pishi, but the situation switched for all greater distances. The Group B Females demonstrated more variability; Jenny, Wanda, Molly and Daisy were more consistently associated with the Adult, Zac; however, Calico showed a preference for her son, Catkin, at close range, as did Laura (along with Carbonel and Dijon) but this changed to Zac at greater distances.

The same absolute value existed between the two members of any one dyad, but this often translated to differences in relative proportions of time with the other cat. The

Figure 3.4.a

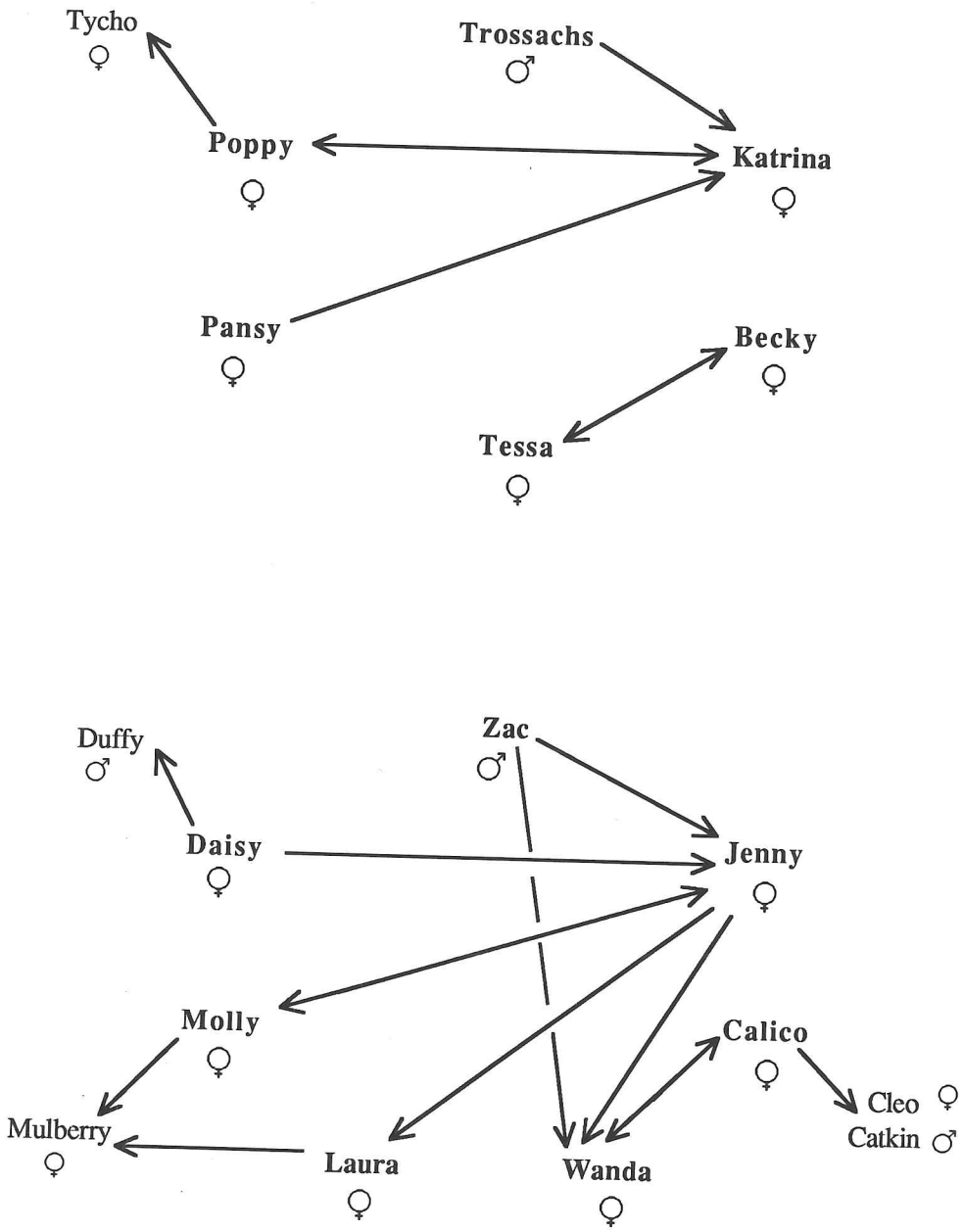


Figure 3.4.a: The most common partners for Contact proximity scans. Arrows reflect the direction of the "preference", such that the Focal individual is at the origin of the line. Where a Juvenile or Kitten was the most common partner, this has been indicated, along with the most frequently seen Adult partner. The top figure is Group A, the bottom figure is Group B.

Figure 3.4.b

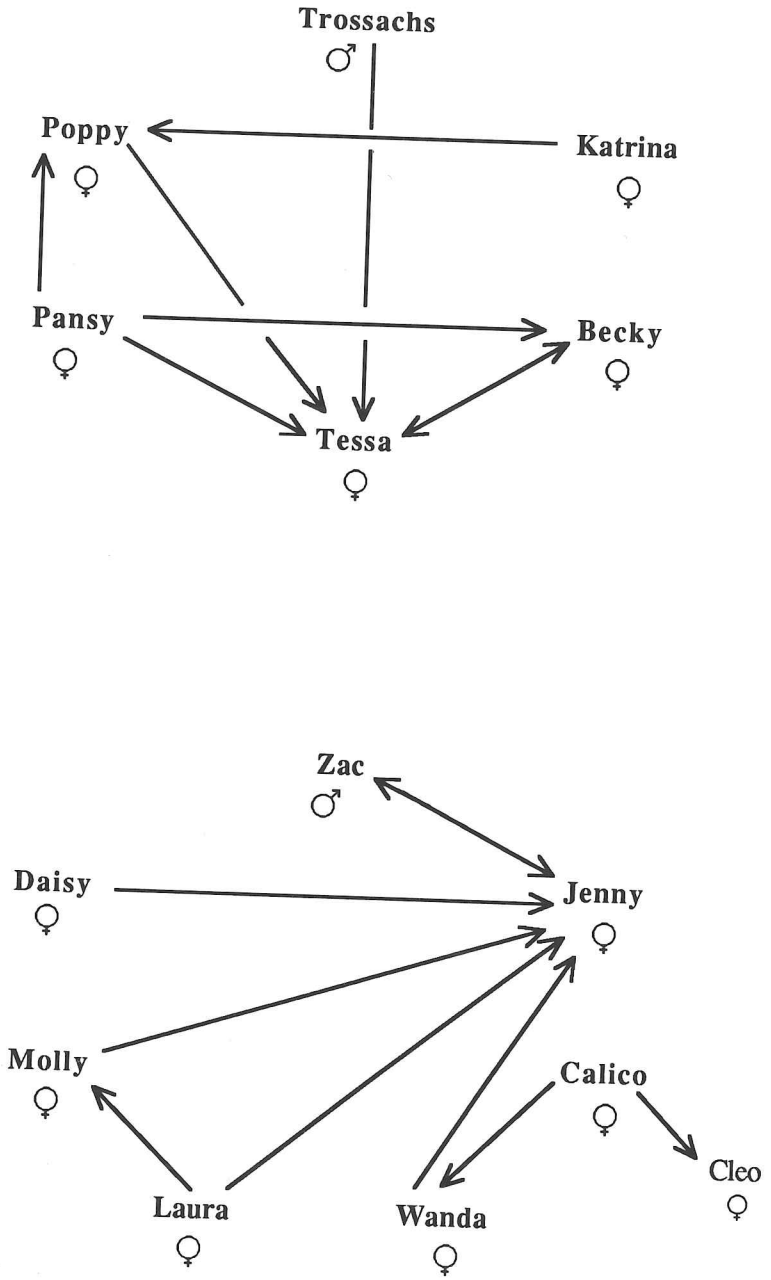


Figure 3.4.b: The most common partners for the sum of all proximity scans, Total to Five Metres. Arrows reflect the direction of the "preference", such that the Focal individual is at the origin of the line. Where a Juvenile or Kitten was the most common partner, this has been indicated, along with the most frequently seen Adult partner. The top figure is Group A, the bottom figure is Group B.

highest score for a Male, for instance, might represent a middle value for a Female. One example of this can be found between Trossachs and Katrina; the weighted value of 1.085 was the maximum for Trossachs in Contact (and denoted Katrina as his preferred partner at this distance), while it was one of the lower scores for Katrina and tied when ranked 9th of 12 possible cats. Therefore, when preferred partners were quoted, the differences in absolute value were largely ignored. Trossachs tended to be in Contact with Katrina most (and she with Poppy), Less than Thirty Centimetres with Poppy (Poppy with Tessa), Thirty Centimetres to One Metre with Tessa (Tessa with Becky), One to Five Metres with Becky (which was reciprocated), and overall with Tessa (while she preferred Becky). A similar situation existed with Zac, who was most in Contact with Wanda (she was with Calico), Less than Thirty Centimetres with Jenny (Jenny with Wanda), Thirty Centimetres to One Metre with Jenny (Jenny with Molly), One to Five Metres with Jenny (which was again reciprocated), and overall with Jenny (also mutual).

Preferred partners have been portrayed diagrammatically in Figures 3.4.a and b, which include Female-Female associations as well as inter-sex ones. Again, it must be emphasised that the absolute size of the weighted value has not been illustrated, otherwise Male-Female relationships would not be included due to small values at closer proximities. Also, where cats preferred non-Adults over other individuals, these non-Adults have also been shown, along with the most preferred Adult (usually only second or third in rank in these cases).

3.3.3. MALE-MALE

A total of 9 Male-Male dyads were involved in the study; initially, these were all Adult-Juvenile, but 5 became Adult-Adult in 1989. The two groups were not considered for cross-fence proximity, as this was felt to be random after the first spate of mutual interest when the cats were released. As mentioned in the previous sections, Adult Males preferred to be around Females rather than other Males, so that Male-Male proximity scores are relatively low. Trossachs, the Group A Adult, was more often seen near the older Male, Pishi, than the youngest Male, Biscuit. Again, the dearth of Males allows a minimum of conclusions to be drawn from this group in particular; Trossachs and Pishi were almost never observed within thirty centimetres of one another, and the peak in sightings was at the greatest distance. Pishi was ranked below all other possible cats except the 1988 Kittens, and of these younger individuals, Biscuit (the Male) was lowest of all. Behavioural observations of avoidance and mild agonism between Trossachs and other Males supported the proximity evidence, in that Males were seldom found near one another, and especially not for any length of time.

Zac, the Side B Adult Male, had a few more possible proximal companions from whom to choose. The four older Males seemed to split into two categories; the first involved Carbonel and Dijon, who had proximity totals equal to that seen for the least preferred Female (Daisy), and were occasionally seen in Contact with Zac, as well as at all other distances. These two Males bore a strong resemblance to Females in their proximity relationships; perhaps this was a partial result of their close distance-relationships with their respective mothers, as pointed out in Section 3.2.4. The remaining Males, Catkin and Doolittle, had extremely low proximity scores, of which most of the total was from long-distance sightings; both Males were occasionally seen within thirty centimetres of Zac, but this could well correspond to only one or two instances while eating or while courting a Female, or when the Males were younger. The 1988-born Males were similarly low for pairings with Zac, and were in the same range of scores as Catkin and Doolittle, with more close-range contributions.

3.3.4. ADULT-JUVENILE

Adult-Juvenile dyads totalled 105, but the majority of these (59, or 56%) became Adult-Adult after a period of observation. Most aspects of Adult-Juvenile proximity relations have been covered in the previous sections, such that Adult Females were mainly seen with Juvenile Females, and close distances accounted for a variable portion of these totals; Bojangles and Brigit were favoured in Group A (except for Poppy, who had a higher score with her daughter, Pippin), with Tycho far preferred to her counterparts among the younger cats. In Group B, Adult Females were closer to Mulberry overall, although several Females preferred their sons to Mulberry. The younger Female, Cleo, had higher scores than other younger cats, except for the association between Duffy and both Molly and Daisy (who reared him).

Adult Male-Juvenile interactions were described in the preceding section for young Males; as for young Females, Adult Males were seen near them in more scans (Trossachs with Bojangles, Zac with Mulberry) than with other Males. Younger Juveniles received a more mixed reception, in that Trossachs preferred a Female (Tycho), while Zac was more often seen with a Male (Duffy); however, Zac was seldom near Duffy, and the young Female, Cleo, ranked highest at close quarters.

3.3.5. JUVENILE-JUVENILE

Quantifiable Juvenile-Juvenile comparisons were not possible in the absence of Focal scans on Juveniles. All information regarding Adults and Juveniles was gained from Adult scans, while Juvenile dyads were incidental anecdotes from Adult observations.

This was supplemented by casual notes on Juvenile affiliations. In Group A, Bojangles and Brigit were commonly seen together, and they tended to have similar scores for proximity to specific Adults; in 1989, Bojangles and Pippin bred together, and Brigit was seldom found near them after that, while Bailey (and later Tycho) joined the coalition. These Juveniles were seen in the same area as one another through most of mid-1989; Pishi and Biscuit, the Males, were more isolated from other cats, although Pishi was often the focus of attention for his younger counterpart.

In Group B, most of the Juveniles spent late 1988 and winter 1989 in common resting areas, with the exception of Mulberry, who had stronger affiliations with some Adult Females. Carbonel was the next to leave the coterie, as he was found increasingly in the region of Adult Females, including his mother; by the breeding season, Catkin had also left, and spent the next month or so in the nest with his mother and her new kittens, plus several younger cats (Cleo, Casey and Duffy). Dijon and Doolittle continued to remain more-or-less together, often resting in the same hut and lurking in the same outer region of the enclosure. By June 1989, most of the young Males had left the group, and data collection ceased.

3.3.6. KITTENS

Kittens were not focally observed during scans but were recorded in two separate senses; Females with young litters were noted as being in Contact or close to the Kittens during the first few weeks. After this, individual Kittens were referred to by name, but were not actually included as proximity partners until October 1988, when they had become resident Juveniles. Before that time, the density of Kittens was too high to reliably keep track of all individuals. Thus, Kitten information is presented in two guises: firstly, as the recipient of Female proximity in terms of own versus other litters (Section 3.3.4); secondly, as a supplement to Juvenile data, where the appellation "Kitten" refers to the year of birth and not the actual age, as will be pointed out where this occurs (Section 3.2.6). Much of the latter data has also been included in previous sections dealing with Juveniles.

3.4. THE INDIVIDUAL

3.4.1. FEMALES

Friedman's analysis of variance was performed over all individuals and all proximities to look for differences (see Section 3.1.2), which proved significant ($\chi_r^2 = 25.846$, $p<0.05$, $df = 12$), with the following rank order: Jenny > Katrina > Poppy

> Becky/Zac > Molly > Calico > Wanda > Trossachs/Laura > Pansy > Daisy. When each group was tested separately, the differences remained in Group A (χ_r^2= 11.571, p<0.05, df= 5) but not within Group B (χ_r^2= 11.357, p= .078, df= 6) If the comparison was repeated using different distance categories, cats showed non-significant disparities when close (χ_r^2= 19.912, p= .069, df= 12; such that Poppy > Calico/Tessa > Jenny > Katrina > Becky/Wanda > Laura > Molly > Pansy > Zac > Trossachs > Daisy); however, the difference was stronger at greater distance (χ_r^2= 22.154, p<0.05, df= 12), with the rank order Jenny > Zac/Tessa > Molly > Trossachs/Poppy > Becky > Wanda > Laura > Katrina > Calico/Daisy > Pansy. Where "rank orders" are given, as here, this is intended solely for insight into the characteristics of individuals (most particularly those at the extremes of the ordering), but do not indicate significant differences between individuals. The Friedman's test compares proximity scores over all the individuals to find the statistic, and cannot be applied to subsets of the tested group. The significance levels should be interpreted with caution, particularly when dealing with comparisons across individuals (matched on some measures, such as proximity categories).

All Females were again tested once Males were removed from the sample; close distance proved non-significant among the Females (χ_r^2= 16.091, p= .097, df= 10), while further distance was markedly different (χ_r^2= 19.636, p<0.05, df= 10) when all Females were considered together. Scores for unavailability were also compared for Females; differences were not significant for either Group or for Females (Table 3.4.a). Thus, whole groups and the Females in each group showed no overall significant differences when all distances were included, but Females varied more when just long distances were considered.

Individuals were compared for the proportion of scans they were seen at close proximity (Figure 3.5); relatively little variation was found with the exception of Daisy, who spent only 7% of scans at less than thirty centimetres from any other cat. Daisy might be described as a solitary cat, who was rarely seen in the core feeding area, or near other Adults. From the overall values, a mean for close proximity was calculated, such that Females spent about 24% of scans near others (slightly more for Group A cats and less for Group B), versus 12% for Males. Correlation analysis was performed on the individual totals for each category (Table 3.4.b), such that cats who spent a lot of time "Near" were less often seen at distances greater than five metres or out-of-sight (e.g. unavailable); cats seen often at longer distances were also generally available for scan purposes, with low numbers of scans when they were greater than five metres away or out-of-sight.

Individuals varied as to when they demonstrated the most sightings at any one distance; some Females were seen in Contact mainly in the cooler winter months (e.g. Katrina, Pansy, Poppy, Jenny, Laura, Daisy), while others peaked during cooperative

Table 3.4.a: Differences in Unavailability (Greater than Five Metres and Out-of-Sight) between Groups and Among Females, Using a Friedman's Analysis of Variance

Groups Involved	**df**	χ_r^2	**p**
Group A	5	8.478	.132
Group B	6	10.500	.105
All Females	10	18.073	.054†
A Females	4	7.282	.122
B Females	5	9.143	.104

†The rank order for Females was: Pansy/Daisy > Laura > Katrina > Molly > Becky/Wanda > Calico > Tessa/Poppy > Jenny. This ordering is provided because of the insight it offers about Females arranged at the extremes of the ranks, but does not mean to imply any statistically significant difference between individuals (the Friedman's test analyses the group as a whole, and the statistic refers only to the complete set).

Table 3.4.b: Correlations of Individual Proximity Totals (n=13). Significant probability levels indicate that the two variables are linearly related when ranked values for each individual cat are compared. For example, cats found often near others were found rarely at greater than five metres (note the negative correlation coefficient).

Proximity 1	**Proximity 2**	r_s	**Z**	**p**	
Near	Far	.099	.343	.732	
Near	> 5 Metres	-.735	-2.545	<0.05	*
Near	Out-of-Sight	-.604	-2.094	<0.05	*
Near	Total Unavailable	-.759	-2.630	<0.01	**
Far	> 5 Metres	-.514	-1.780	.075	
Far	Out-of-Sight	-.632	-2.189	<0.05	*
Far	Total Unavailable	-.586	-2.030	<0.05	*

breeding (e.g. Becky and Tessa, Wanda, Molly). Less than Thirty Centimetres also displayed these differences between winter aggregations (e.g. Katrina, Becky, Pansy, Poppy, Calico) and breeding ones (e.g. Tessa, Wanda, Laura, Molly, as well as the non-cooperating Jenny and Daisy). Longer distances were more uniform, and were highest in summer to early autumn. Other seasonal aspects will be more fully discussed in Section 3.5.

3.4.2. MALES

Of all the Adult individuals, Males spent the lowest proportions of their observations at close proximity to others (Figure 3.5.a), therefore demonstrating higher values for further distance scores. Trossachs spent 91% of his scans at distances greater than thirty centimetres, while Zac spent 86%; these values were larger than for any Female other than Daisy, who also showed a very small proportion of time at close proximity (Figure 3.5.b). Of these two Males, Zac was seen more often in Contact and close to other cats, while Trossachs had extremely low scores, especially for Contact. Out-of-Sight scans were not as prevalent (for "unavailable" scores) as those at Greater than Five Metres for most Adults (Figure 3.5.c).

The two Males had similar general temporal patterns for proximity, with a peak for close distances in cooler months, probably resulting from huddling for warmth; middle distances (from fifteen centimetres for Zac) were highest in the summer months, when Females were in breeding groups and the cats often remained near the core area. The greatest range, up to five metres, peaked in early winter, after the Kittens had matured slightly and before the winter weather grew too harsh for general activity. Weather effects and seasonality are further described in Section 3.5.

3.4.3. JUVENILES

Preferred partners were considered for all Adults toward Juveniles; in Group A, Bojangles was the favoured proximity partner, and her allomother, Poppy, contributed the highest score to this value. In Group B, Mulberry was the focal proximity Juvenile, and, again, her mother, Molly was responsible for the largest portion of the sightings.

Individual Juveniles were seen at different sets of distances, in that some were relatively frequently in Contact, while others were often seen at distances greater than one metre. The specific Adult partner also influenced these proportions. For example, Bojangles was seen at less than one metre as often as at greater than one metre for Katrina, Pansy and Poppy, while the further scores were much higher for Trossachs, Becky and

Figure 3.5.a

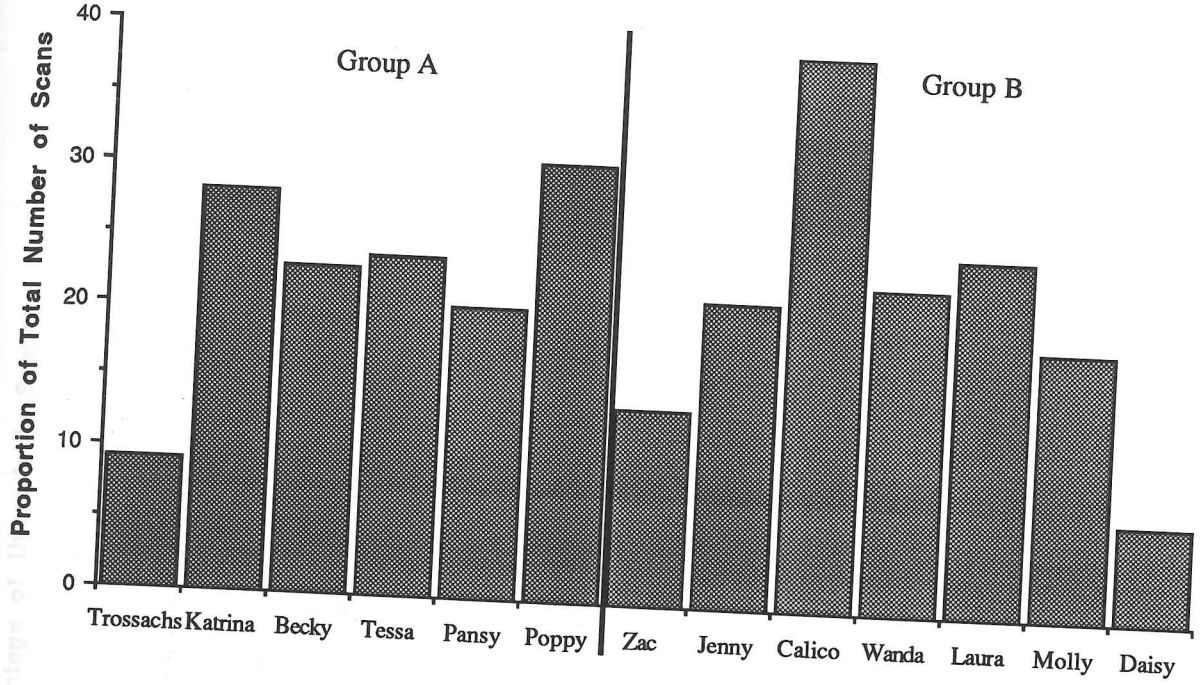


Figure 3.5.b

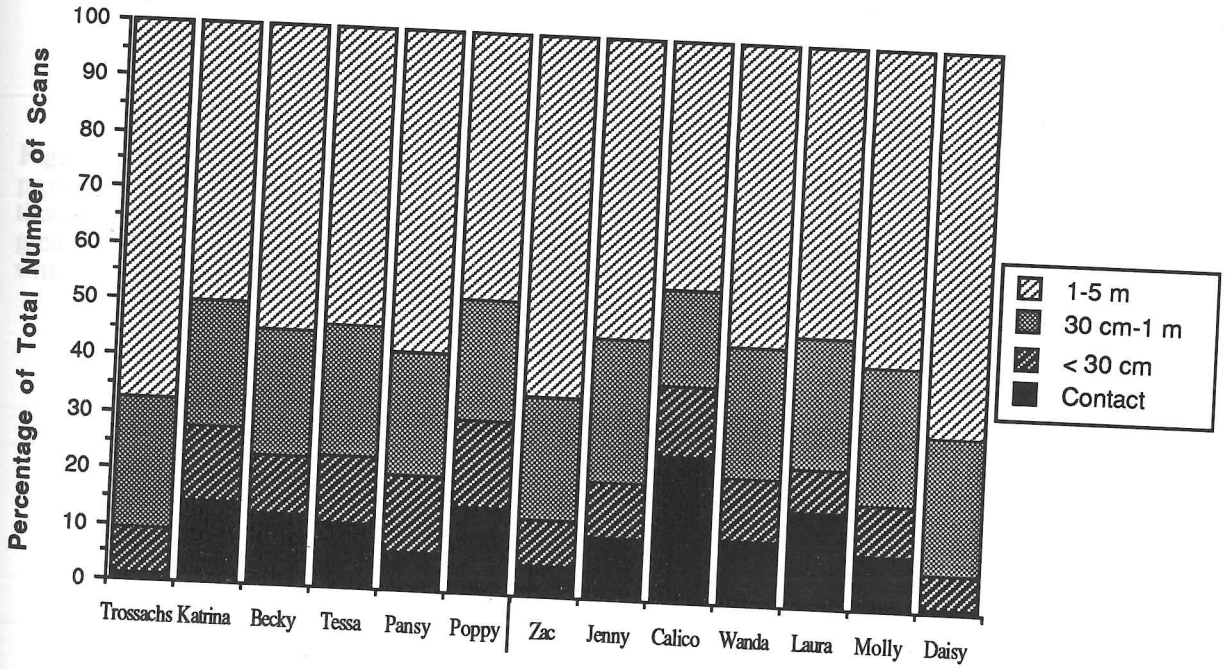


Figure 3.5: Individual differences in proximity measures. Values are presented as the percentage of all proximity scans in which the focal individual was seen within 5 metres of another cat. (**a**) Total at close distances, including Contact and Less than 30 centimetres; (**b**) Summary of totals for each distance category. Measures for "unavailable" scans (e.g. > 5 metres and out-of-sight) could not be included in this summary, as they were not subject to the same weighting considerations (due to the lack of a possible dyadic structure). These "unavailable" scores are presented in Figure 3.5.c; they contributed less than ten percent of scans for most Adult cats (with the possible exception of Daisy, who may have been as high as 25-30%).

Figure 3.5.c

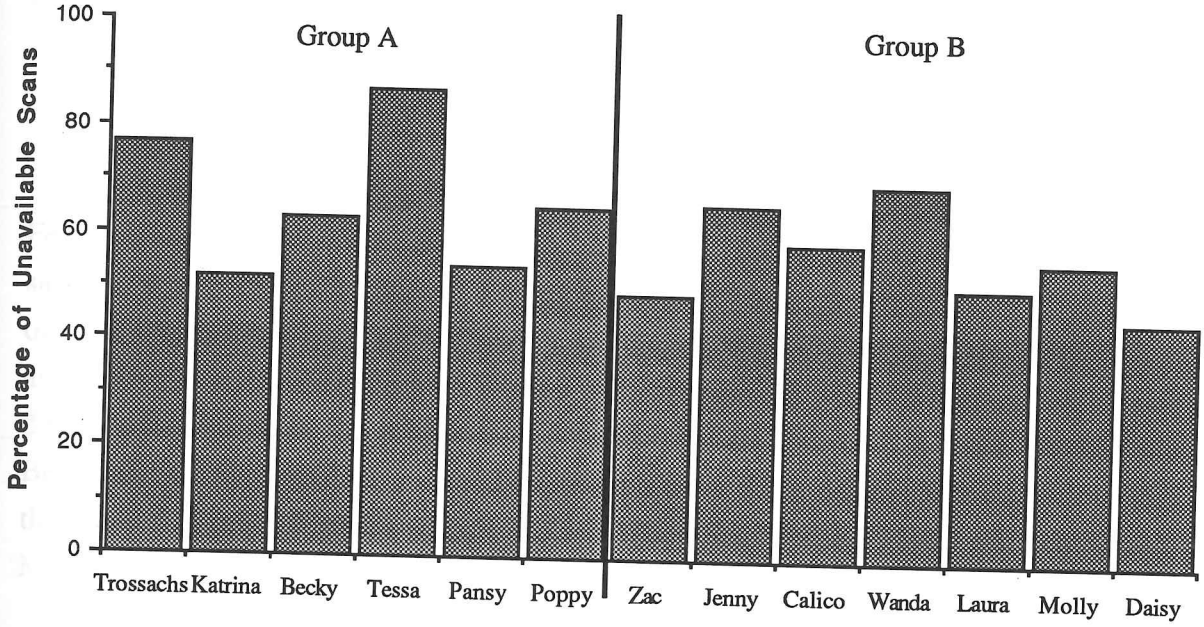


Figure 3.5: Individual differences in proximity measures. Values are presented as the percentage of all proximity scans in which the focal individual was not seen within 5 metres of another cat and was therefore scored as "Unavailable". (c) Percentage of unavailable scans in which the individual was greater than 5 metres away from all other cats; the remainder (to 100%) was contributed by scans in which the focal cat was out of sight.

Tessa. In this sense, Pippin, along with Carbonel, Catkin, Dijon, and occasionally Mulberry (for Laura and Molly) and Bojangles were more closely affiliated with most Adults; the remaining cats, Brigit, Pishi and Doolittle, had few close associations with Adults, and were primarily seen at more casual distances.

When the same comparison was run for younger Juveniles, Biscuit, Bailey, Tycho, Casey, Cleo, and sometimes Dickory and Duffy, all had close-range proximity associations with Adults, and were less often seen at greater distances.

3.4.4. KITTENS

Kittens, unsurprisingly, were often found in the immediate vicinity of Adult Females, and were less often seen with Adult Males. Young Kittens were predominantly sampled at very close distances to their mother and any helpers; within four or five weeks of birth, they became more mobile, and longer range scans were increasingly likely. When all observations of a Female with Kittens were considered, within 5 metres, individuals displayed variation in the proportion of sightings with their own Kittens. Some, like Becky and Daisy, were predominantly with their own, while others spent more time near the Kittens of other Females (Figure 3.6.a). When Females and Males were compared, Males were seen only rarely with Kittens, and this only at some distance (Figure 3.6.b).

A strong relationship was seen between the identity of a Female and the amount of time spent with own Kittens (χ_r^2= 23.144, $p<0.01$, df= 8), but the differences were not as striking when considering time with other Kittens, e.g. not their own litter (χ_r^2= 16.663, p=.082, df= 10). These tests were performed using Females as blocks and proximity categories as matched variables The significance levels should be interpreted with caution, particularly when dealing with comparisons across individuals (matched on some measures, such as the proximity categories used here), but are useful indicators of large differences among individuals. An interesting feature was shown when Females were ranked for the two measures: some individuals spent relatively large amounts of time with Kittens, regardless of identity (Calico, Wanda), some preferred only their "own" offspring (Becky, Tessa, Daisy), and several appeared to negatively discriminate against their own and were more commonly with other Kittens (Jenny, Katrina).

When analysis was performed over all Females, to test for a preference for a particular type of Kitten (see Section 3.1.2), significant differences were found for each group (Side A: χ_r^2= 67.393, $p<0.001$, df= 4; Side B: χ_r^2= 132.047, $p<0.001$, df= 5) and over all Females (χ_r^2= 199.44, $p<0.001$, df= 10). The actual distances involved also varied among the Females, with closer proximity (especially Contact in the case of pre-weaning Kittens) discriminating between casual and specific interactions.

Figure 3.6.a

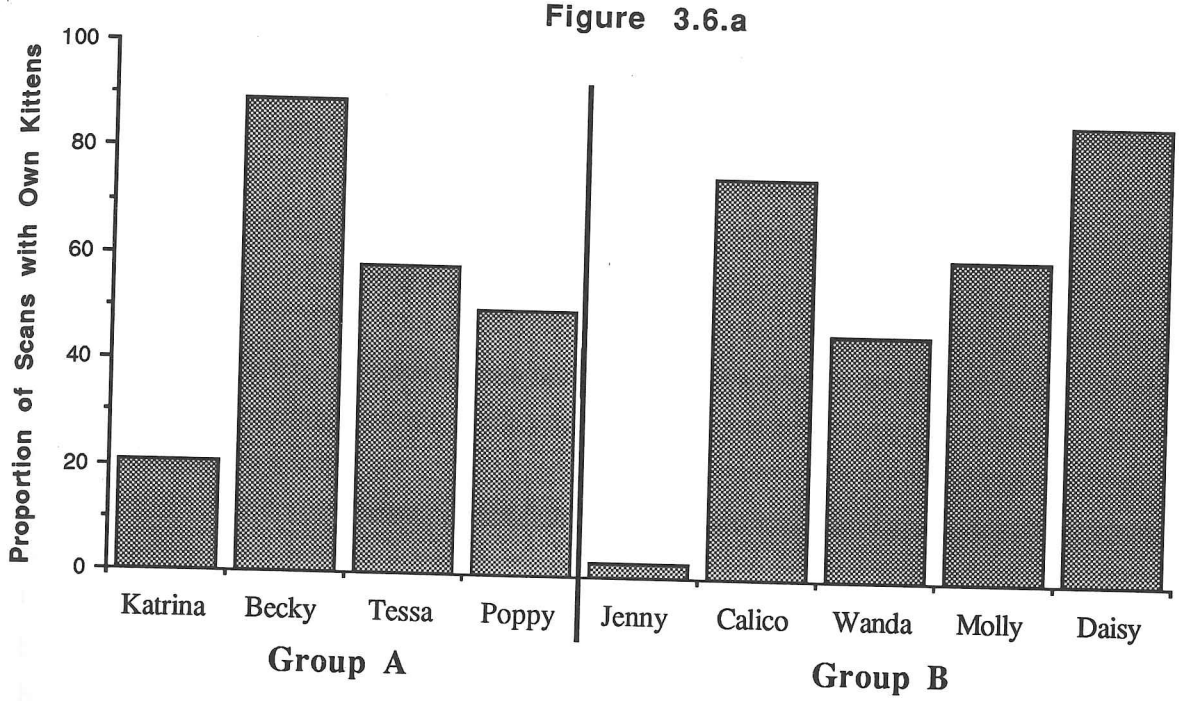


Figure 3.6.b

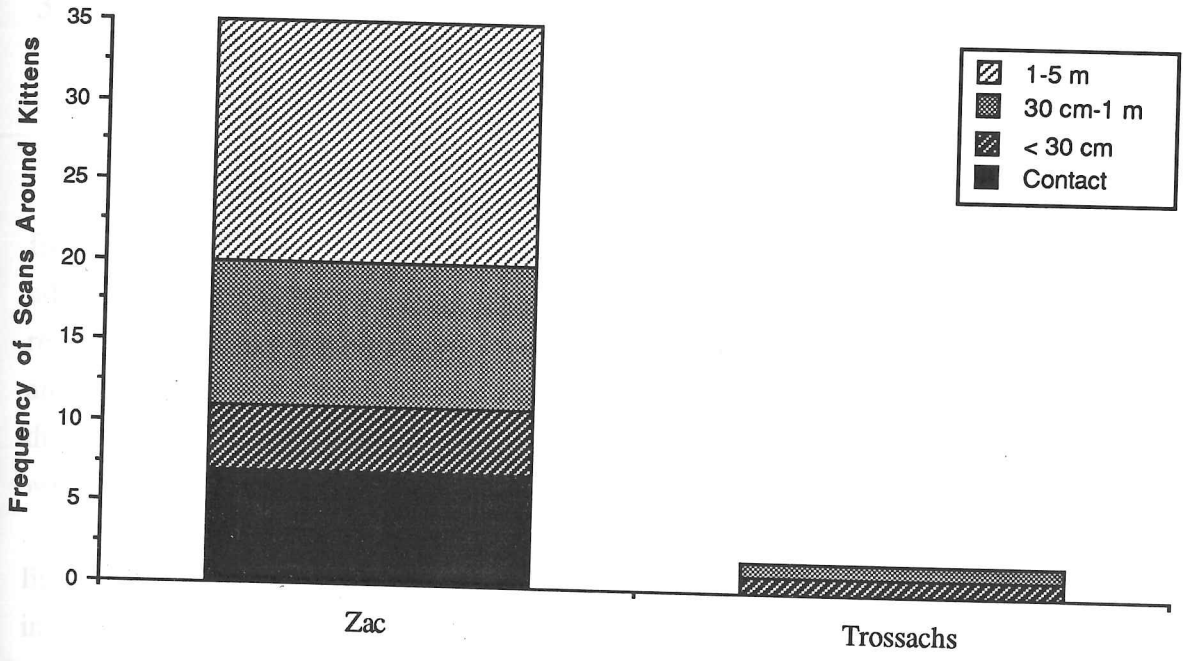


Figure 3.6: Proximity to Kittens. (a) The proportion of all scans (within 5 metres) that Females were with their own Kittens (versus other Kittens); (b) Males and their total proximity to any Kittens.

The vast majority of observations were made of cats in contact (79%) and also with their own offspring (54%). Relationships between breeding Females may be rendered more obvious by looking at the spatial interactions with Kittens; Katrina, who had a combined litter with Poppy but who abandoned her portion of the care after several weeks, spent a scant half of her time with the joint litter and was seen with Becky and Tessa's litter in the remaining time. Tessa, who reared a communal litter with Becky in 1988, was often, in 1989, found with Becky's subsequent litter (50% of her remaining time near any Kittens). As for the non-breeding Females, Pansy preferred Poppy's Kittens (44%), and Laura was strongly attracted to the combined offspring of Molly and her daughter Mulberry (72%).

When preferred partners were considered overall, Tycho was the favoured Kitten in Group A, and the strongest proximity link between her and an Adult was with Poppy; this may have been the result of Poppy and Tycho's roles as allomothers for a litter by Becky in 1989, and not due to actual association while Tycho was a Kitten. In Group B, Cleo was the most preferred, and her mother, Calico, contributed most to this score.

3.5. SEASONALITY

3.5.1. METHODS

There were two separate methods by which seasonality was defined. The first of these was subdivision into months of the year; previous studies have attempted to address the possibility of cyclic changes in individual behaviour, including proximity relationships, using monthly totals. It is unlikely that behaviour patterns, and the weather, are as sensitive to the Julian calendar as observers, and so this first method is included for the purposes of comparison, and offers a simple basis for contrast. The second technique was slightly more complex.

Each Female was assigned a reproductive status, based on the birth date of litters. The "seasons" thus found correspond to a similar reproductive state for each Focal individual, although the weeks which accord to each season are not absolutely the same across all animals. The seasons were defined in the following way: GESTATION was the 65 days preceding the birth of a litter (in practical terms, it was often calculated by summing over 10 weeks, to yield some flexibility to the period); BREEDING was dated from the birth of a litter to one of several possible outcomes, including the death of the litter, a subsequent gestation period, or three months from the birth of a surviving litter; WINTER was the non-reproductive period, prior to a gestation term and following from a breeding season. For many Females, this system divided the year into five discrete blocks:

$Gestation_1$, $Breeding_1$, $Gestation_2$, $Breeding_2$, and Winter, often with small gaps between January 1st and $Gestation_1$, and between $Breeding_1$ and $Gestation_2$.

The primary reason for considering each Female independently was the extreme spread of birth dates over the year; while the majority fell into fairly synchronous "seasons", the few that did not were biased heavily by a lumped system, especially Calico, who consistently bred a month before other mothers. When the duration of each "season" was found for all Females (Figure 3.7.a), gestation and the first breeding period were of roughly equal duration, while second breeding times were considerably shorter. As mentioned in Section 3.1.2, both individual and dyadic totals (over the entire period of data collection) were used in this analysis of seasonal differences. Monthly and weather analyses used all distance measures and "Near" versus "Far". The main body of analysis, on reproductive seasons, was performed using three categories: "Near", "Mid" and "Far".

3.5.2. RESULTS

When all Adults were examined for the month in which they showed the greatest levels of each proximity, surprisingly little variation was found; Contact was highest, generally, in March 1988, although communal Females varied somewhat, probably due to the dates of more cooperative breeding efforts. All other proximities tended to peak in July 1988, which, along with the preceding June, was the month of maximum cat density and included Kittens for the first time (only the seven Kittens who remained throughout the rest of the study were included in the proximity measures). Group B did display somewhat more variability, however, and individuals peaked at different times throughout the eighteen months of data collection.

"Near" and "Far" proximity totals were correlated across all relevant months from the same year and the next year, to look for general patterns relevant to weather and other factors (Table 3.5.a and Figures 3.7.b-j). Different arrangements resulted for the separate distances; close proximity showed far fewer correlations, and these mainly divided into two groups which appeared to correspond to winter and breeding/summer. Greater distances were less clear, with a large number of correlations between various month elements; linkages were found between all combinations, and it seemed that longer distances were less responsive to changes in circumstances (e.g. were less directly reflecting an underlying social structure with a seasonal component). Altogether, there appeared to be strong cause to move from monthly considerations to seasons based on reproductive state (which crossed monthly boundaries to reflect any changes).

The distribution of months for each proximity category was non-random for "Near" (χ_r^2= 61.584, $p<0.001$, df= 16) and "Far" (χ_r^2= 140.169, $p<0.001$, df= 16), using months as blocks and distance categories as matched variables. The highest ranks

Figure 3.7.a

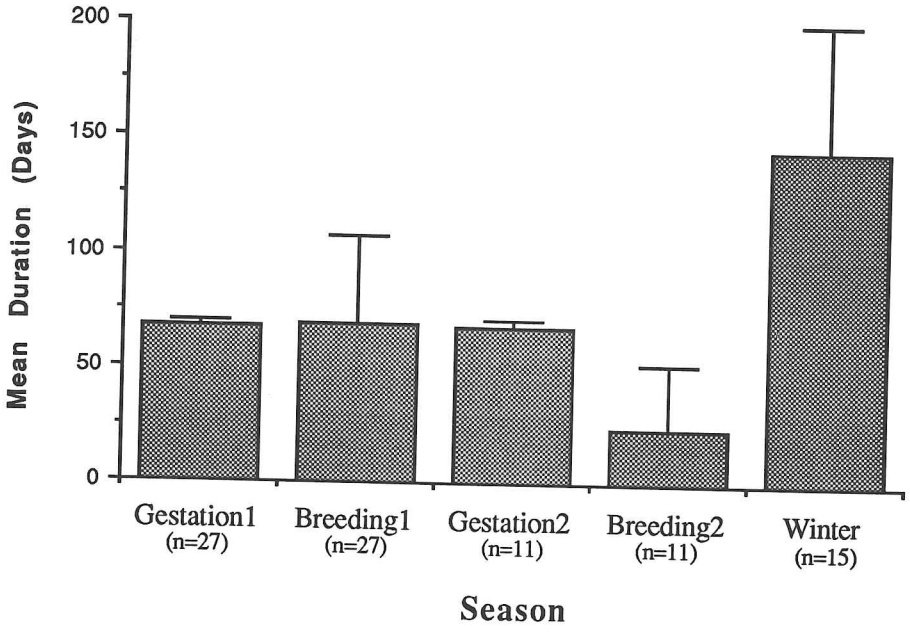


Figure 3.7.a: The mean duration of each reproductive season. Values given are means and standard deviations. The sample size for each group is given as n. Definitions of each season are given in Section 3.5.1; the first measures (marked with "1") correspond to first litters in the year, while measures denoted as "2" are second litters in the same year.

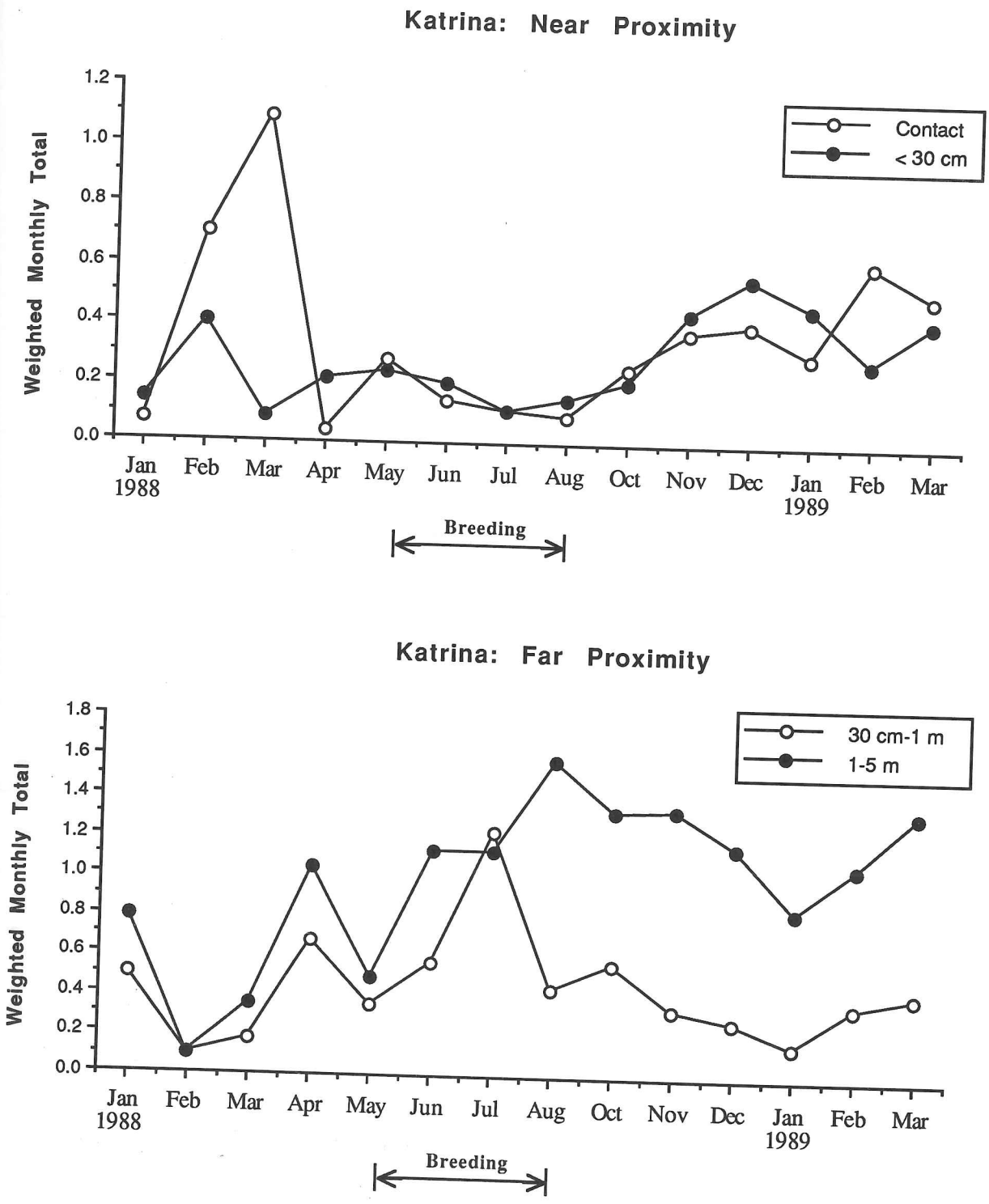


Figure 3.7.b: Weighted proximity data for **Katrina**, shown for each month of proximity observation from January 1988 to March 1989, given as a supplement to Table 3.5.a. The top figure shows the "Near" proximity, with Contact and Less than 30 Centimetres. The bottom figure shows the "Far" proximity, with 30 Centimetres to 1 Metre and 1 to 5 Metres. The Breeding period is indicated at the base of each figure, from the birth of a litter to the subsequent Gestation or Winter. Note the absence of September 1988, due to a lack of observations. Katrina is the only breeding Female with curtailed observations in 1989; this was due to her sudden death in late March 1989.

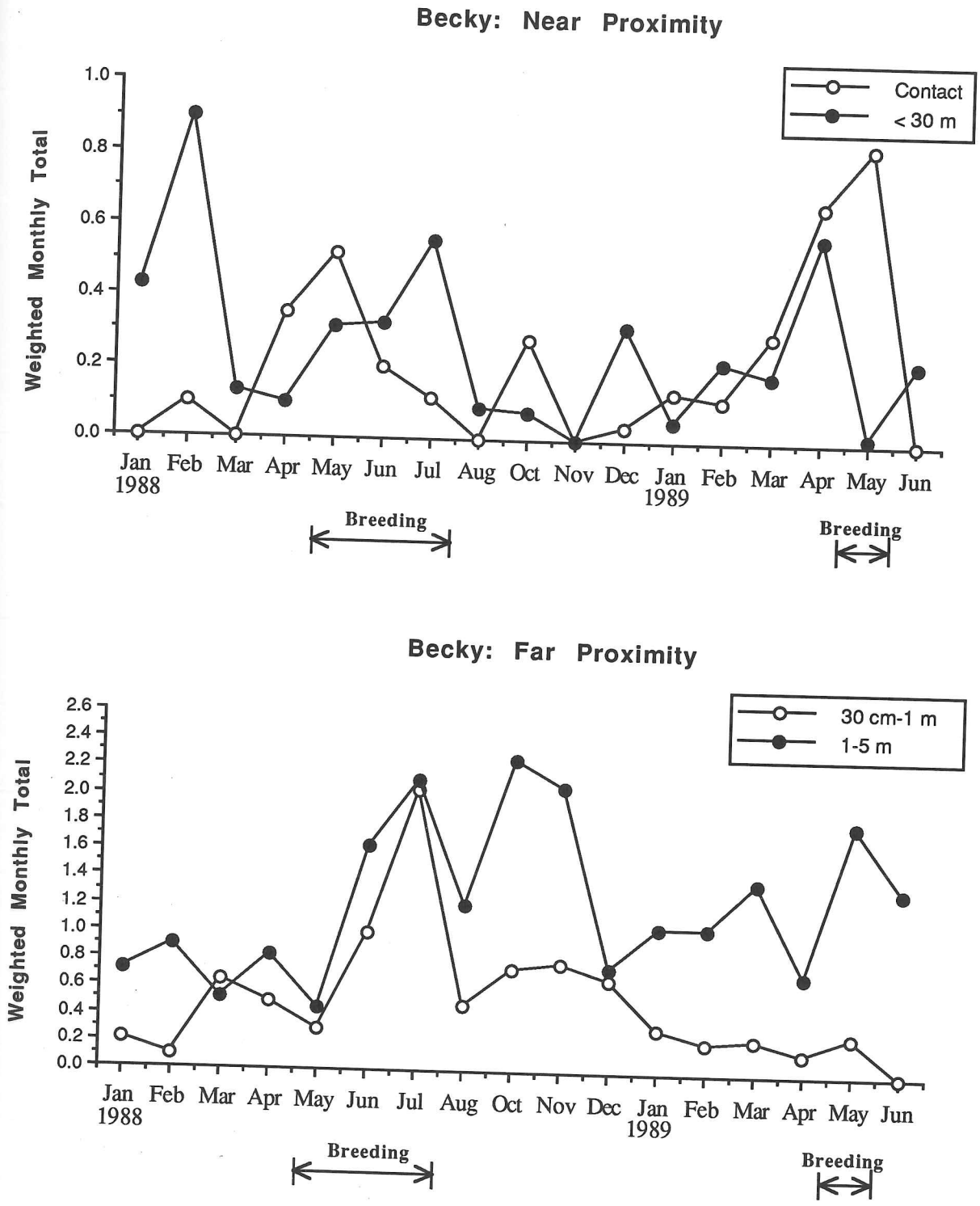


Figure 3.7.c: Weighted proximity data for **Becky**, shown for each month of proximity observation from January 1988 to June 1989, given as a supplement to Table 3.5.a. The top figure shows the "Near" proximity, with Contact and Less than 30 Centimetres. The bottom figure shows the "Far" proximity, with 30 Centimetres to 1 Metre and 1 to 5 Metres. Any Breeding periods are indicated at the base of each figure, from the birth of a litter to the subsequent Gestation or Winter. Note the absence of September 1988, due to a lack of observations.

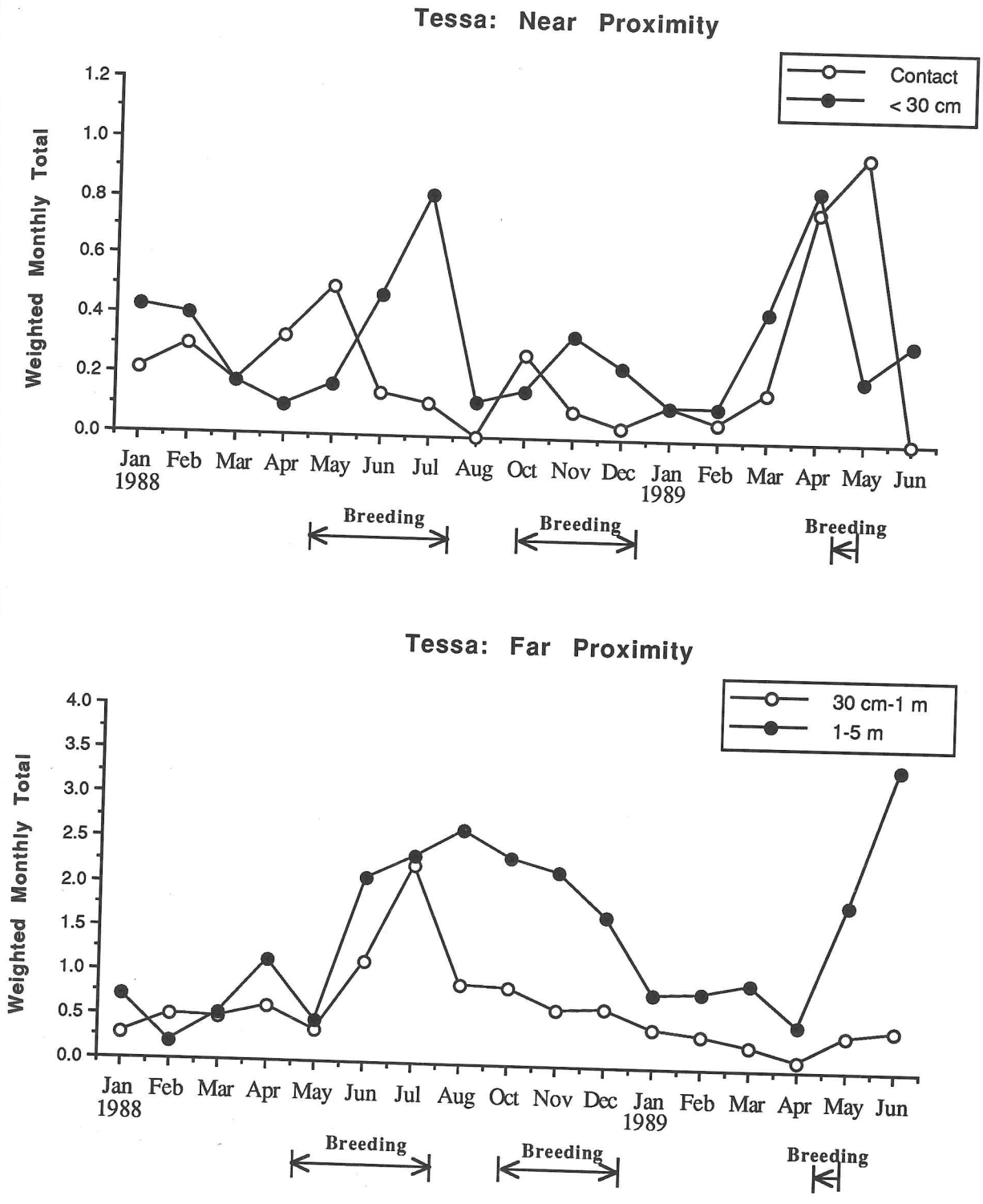


Figure 3.7.d: Weighted proximity data for **Tessa**, shown for each month of proximity observation from January 1988 to June 1989, given as a supplement to Table 3.5.a. The top figure shows the "Near" proximity, with Contact and Less than 30 Centimetres. The bottom figure shows the "Far" proximity, with 30 Centimetres to 1 Metre and 1 to 5 Metres. Any Breeding periods are indicated at the base of each figure, from the birth of a litter to the subsequent Gestation or Winter. Note the absence of September 1988, due to a lack of observations.

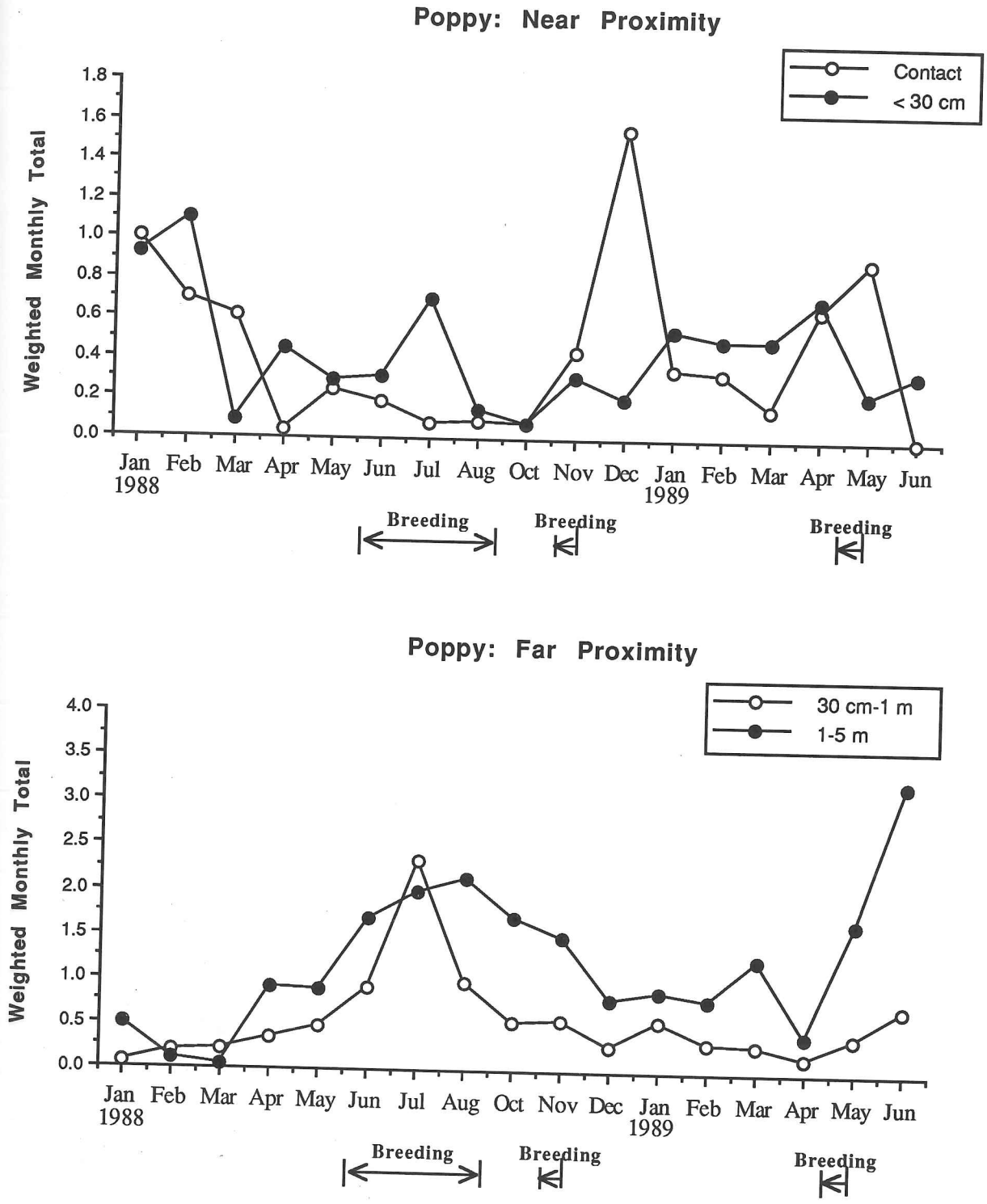


Figure 3.7.e: Weighted proximity data for **Poppy**, shown for each month of proximity observation from January 1988 to June 1989, given as a supplement to Table 3.5.a. The top figure shows the "Near" proximity, with Contact and Less than 30 Centimetres. The bottom figure shows the "Far" proximity, with 30 Centimetres to 1 Metre and 1 to 5 Metres. Any Breeding periods are indicated at the base of each figure, from the birth of a litter to the subsequent Gestation or Winter. Note the absence of September 1988, due to a lack of observations.

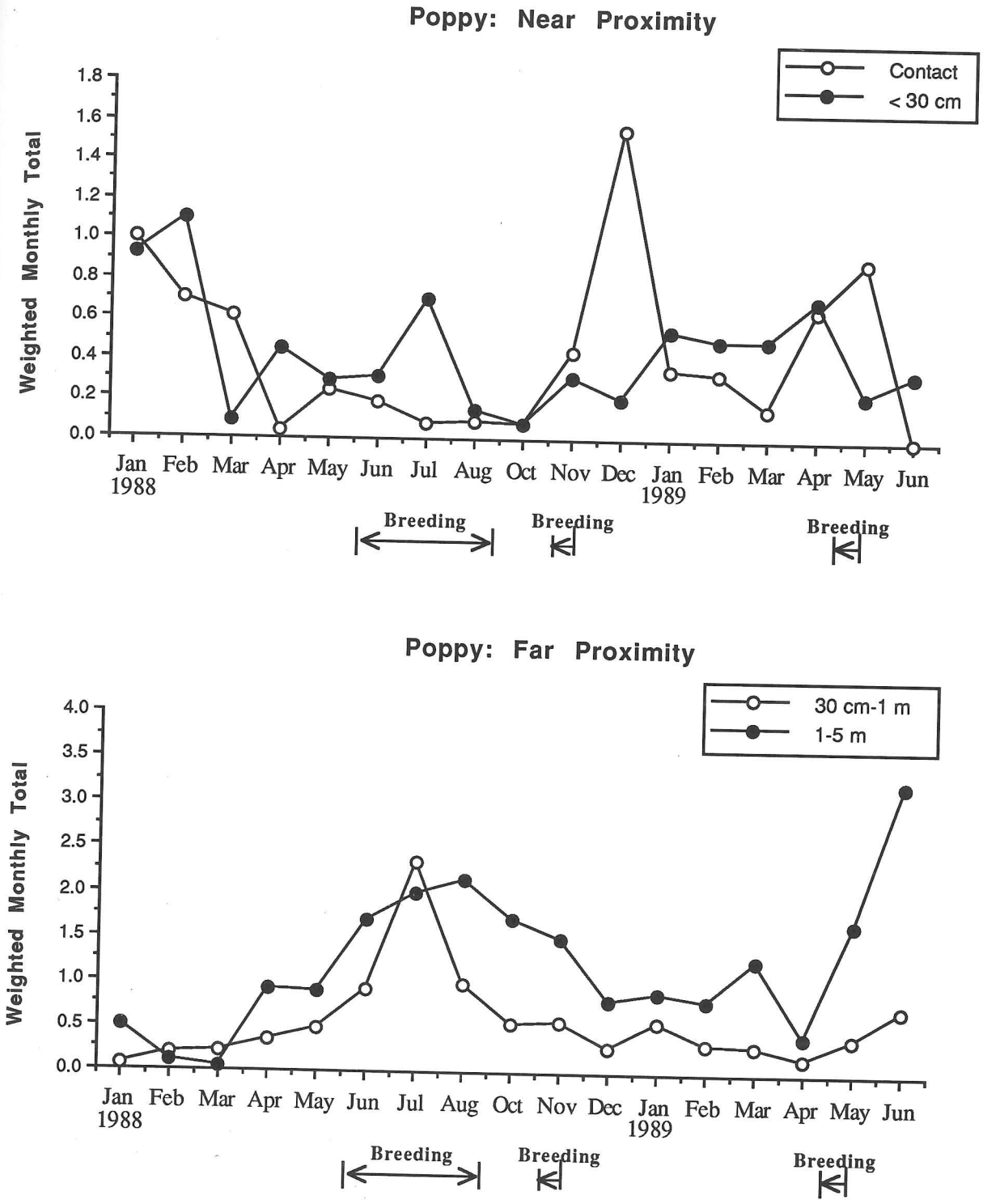


Figure 3.7.e: Weighted proximity data for **Poppy**, shown for each month of proximity observation from January 1988 to June 1989, given as a supplement to Table 3.5.a. The top figure shows the "Near" proximity, with Contact and Less than 30 Centimetres. The bottom figure shows the "Far" proximity, with 30 Centimetres to 1 Metre and 1 to 5 Metres. Any Breeding periods are indicated at the base of each figure, from the birth of a litter to the subsequent Gestation or Winter. Note the absence of September 1988, due to a lack of observations.

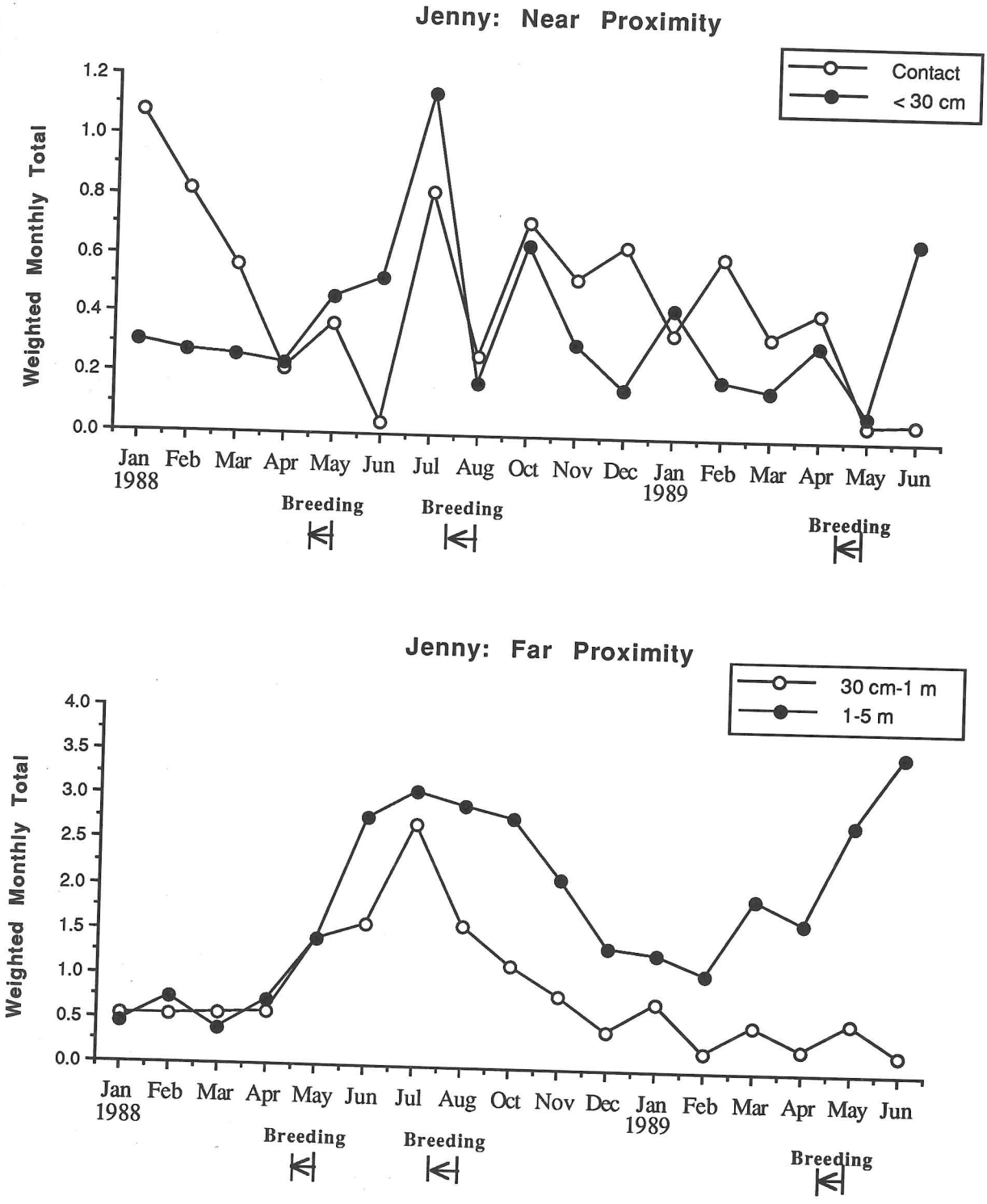


Figure 3.7.f: Weighted proximity data for **Jenny**, shown for each month of proximity observation from January 1988 to June 1989, given as a supplement to Table 3.5.a. The top figure shows the "Near" proximity, with Contact and Less than 30 Centimetres. The bottom figure shows the "Far" proximity, with 30 Centimetres to 1 Metre and 1 to 5 Metres. Any Breeding periods are indicated at the base of each figure, from the birth of a litter to the subsequent Gestation or Winter. Note the absence of September 1988, due to a lack of observations.

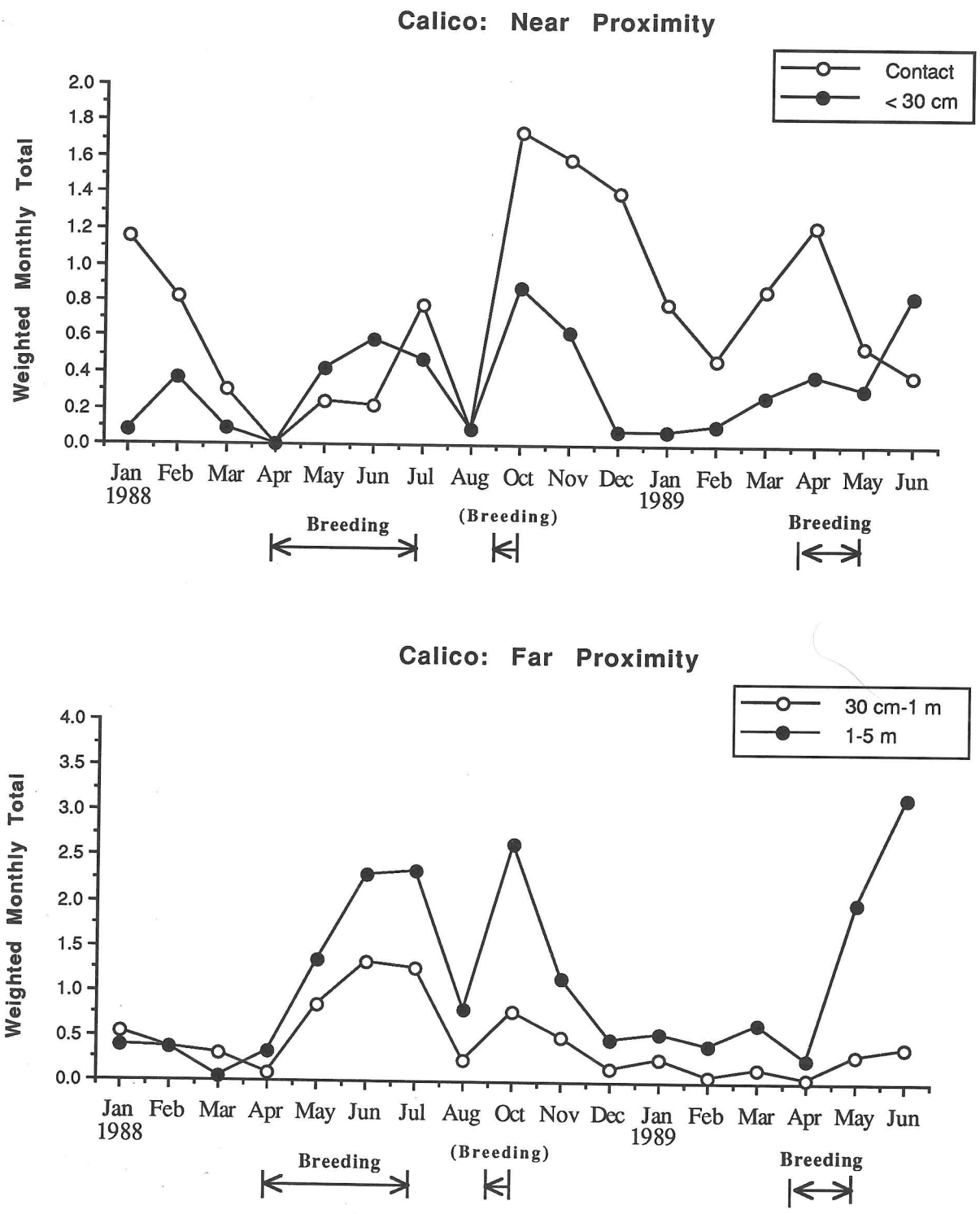


Figure 3.7.g: Weighted proximity data for **Calico**, shown for each month of proximity observation from January 1988 to June 1989, given as a supplement to Table 3.5.a. The top figure shows the "Near" proximity, with Contact and Less than 30 Centimetres. The bottom figure shows the "Far" proximity, with 30 Centimetres to 1 Metre and 1 to 5 Metres. Any Breeding periods are indicated at the base of each figure, from the birth of a litter to the subsequent Gestation or Winter. Note the absence of September 1988, due to a lack of observations. The Breeding period in brackets corresponds to a litter born in September 1988, which died soon after birth.

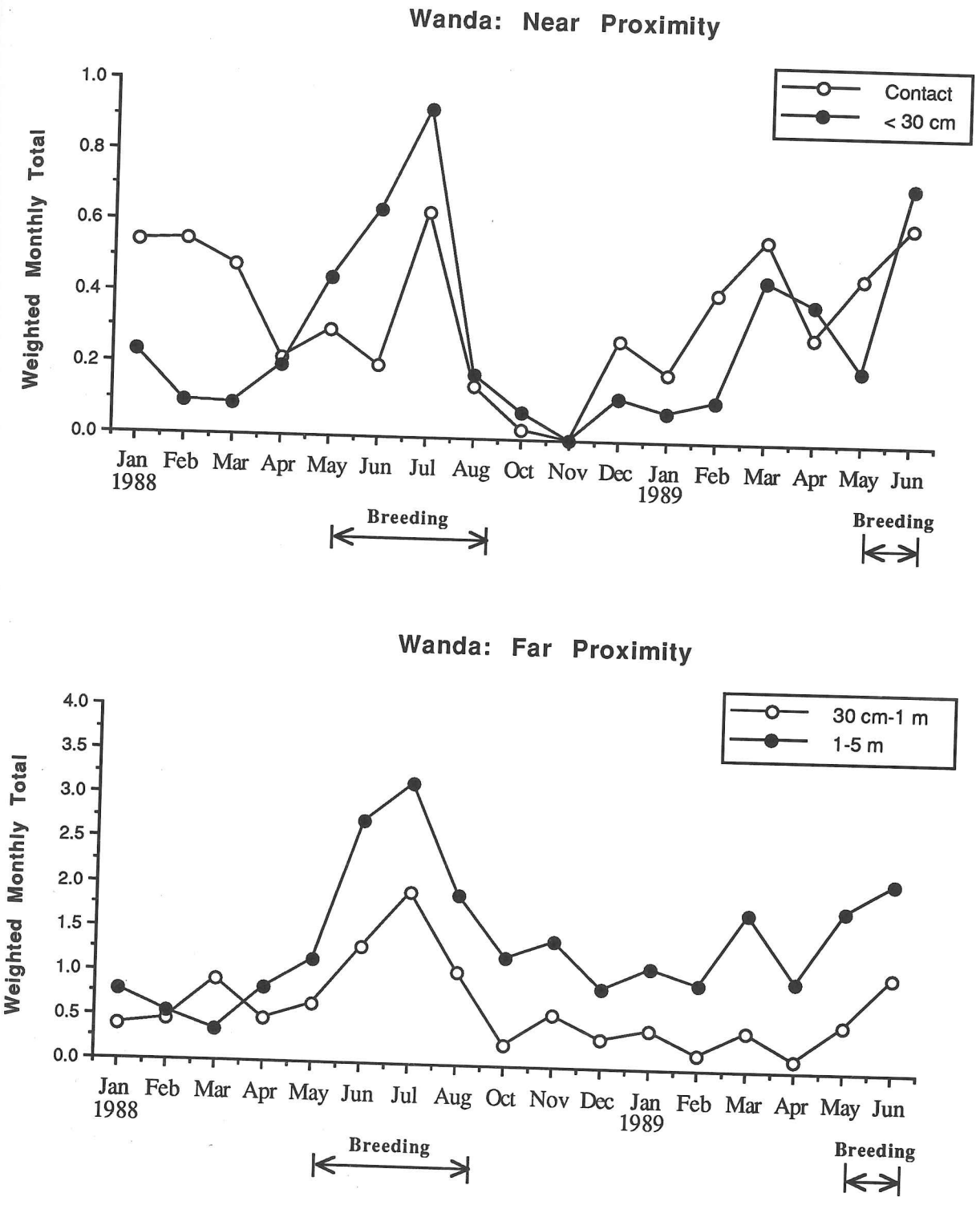


Figure 3.7.h: Weighted proximity data for **Wanda**, shown for each month of proximity observation from January 1988 to June 1989, given as a supplement to Table 3.5.a. The top figure shows the "Near" proximity, with Contact and Less than 30 Centimetres. The bottom figure shows the "Far" proximity, with 30 Centimetres to 1 Metre and 1 to 5 Metres. Any Breeding periods are indicated at the base of each figure, from the birth of a litter to the subsequent Gestation or Winter. Note the absence of September 1988, due to a lack of observations.

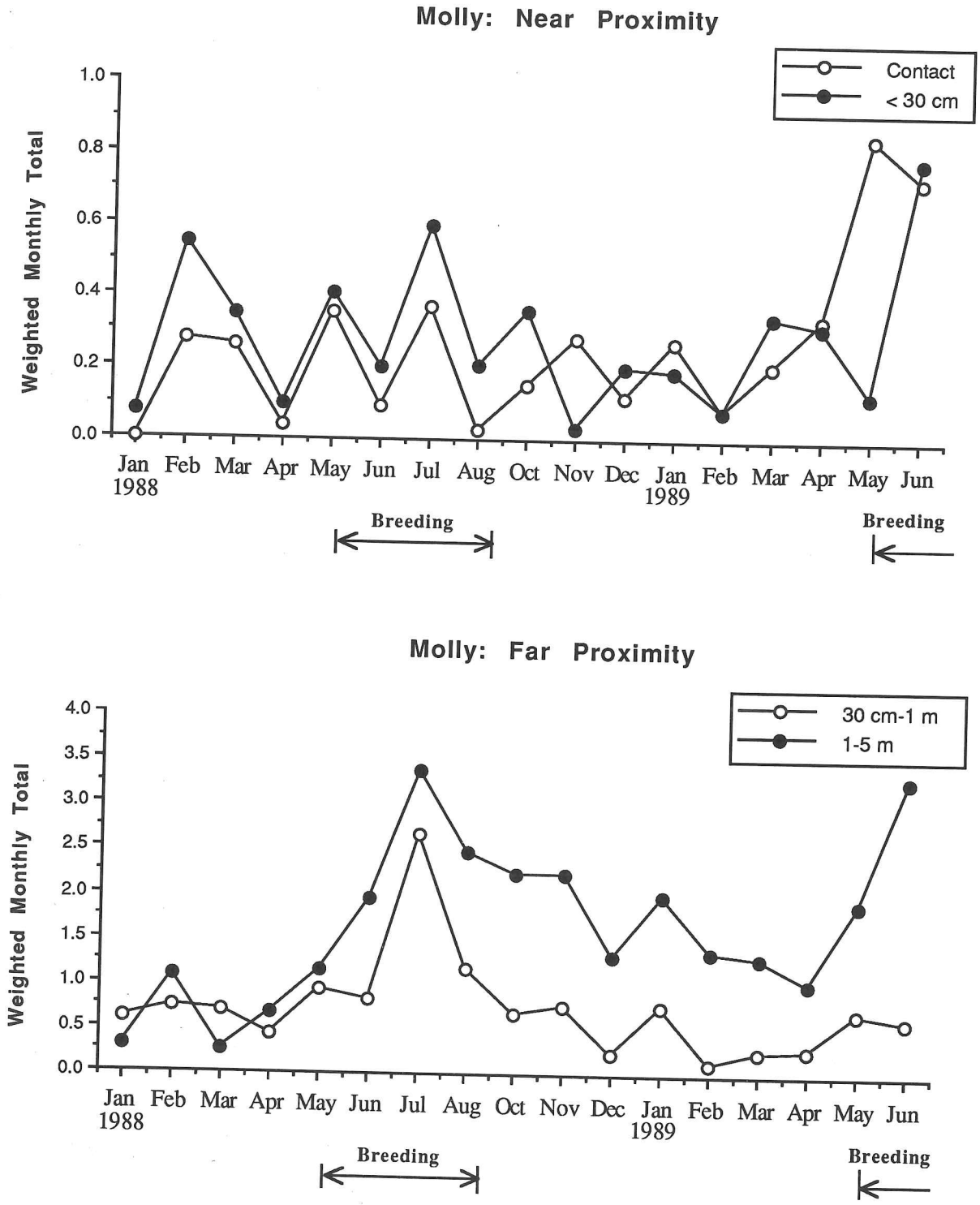


Figure 3.7.i: Weighted proximity data for **Molly**, shown for each month of proximity observation from January 1988 to June 1989, given as a supplement to Table 3.5.a. The top figure shows the "Near" proximity, with Contact and Less than 30 Centimetres. The bottom figure shows the "Far" proximity, with 30 Centimetres to 1 Metre and 1 to 5 Metres. Any Breeding periods are indicated at the base of each figure, from the birth of a litter to the subsequent Gestation or Winter. Note the absence of September 1988, due to a lack of observations.

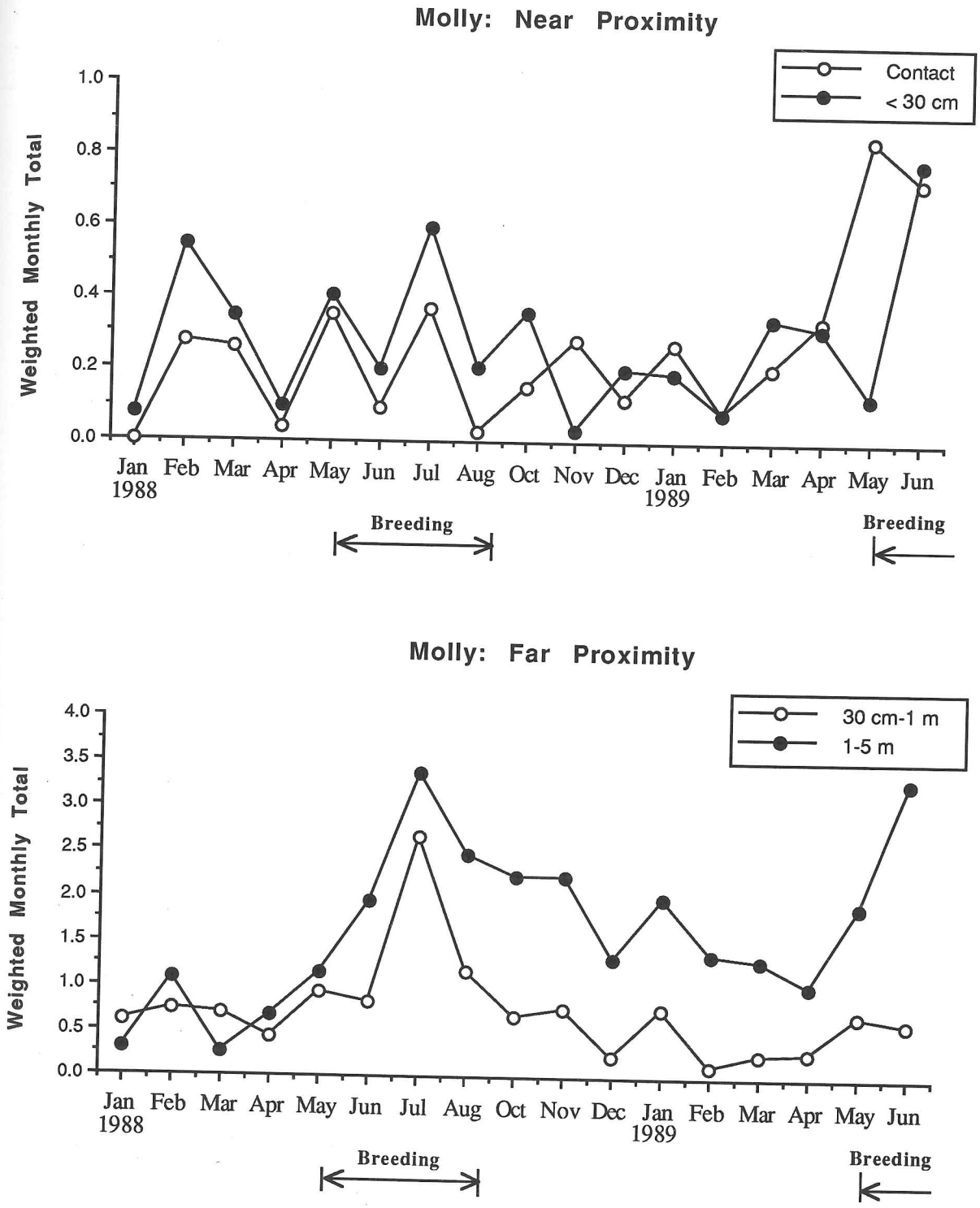


Figure 3.7.i: Weighted proximity data for **Molly**, shown for each month of proximity observation from January 1988 to June 1989, given as a supplement to Table 3.5.a. The top figure shows the "Near" proximity, with Contact and Less than 30 Centimetres. The bottom figure shows the "Far" proximity, with 30 Centimetres to 1 Metre and 1 to 5 Metres. Any Breeding periods are indicated at the base of each figure, from the birth of a litter to the subsequent Gestation or Winter. Note the absence of September 1988, due to a lack of observations.

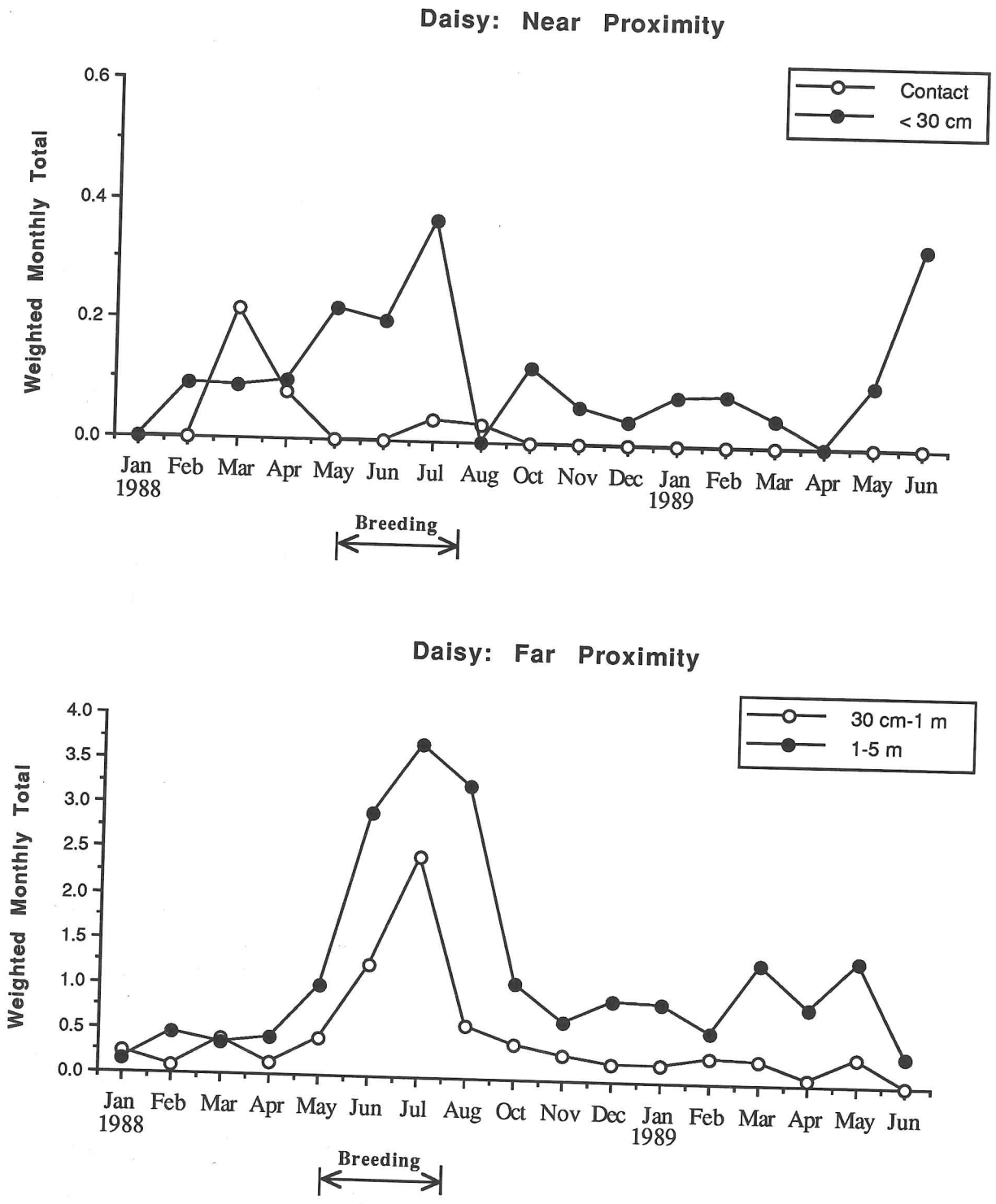


Figure 3.7.j: Weighted proximity data for **Daisy**, shown for each month of proximity observation from January 1988 to June 1989, given as a supplement to Table 3.5.a. The top figure shows the "Near" proximity, with Contact and Less than 30 Centimetres. The bottom figure shows the "Far" proximity, with 30 Centimetres to 1 Metre and 1 to 5 Metres. Any Breeding periods are indicated at the base of each figure, from the birth of a litter to the subsequent Gestation or Winter. Note the absence of September 1988, due to a lack of observations.

Table 3.5.a: Monthly Correlations for Proximity Scores (n=26). Significant probabilities mean that the two months tested are linearly related for the ranks of individual Adult cats. Note that, due to the large number of variables tested together, significant values should be taken as indicative and not absolute. The two "Far" categories (together) show more correlations, perhaps reflecting the more general nature of these distance relationships (not tied to weather or season). Monthly values are plotted for each breeding Female in the preceding Figures (3.7.b-j).

	NEAR				FAR			
Months	r_s	Z	p		r_s	Z	p	
Jan88-Jan89	.365	1.827	.068		.395	1.977	<0.05	*
Feb88-Feb89	.701	3.503	<0.001	***	.333	1.664	.096	
Mar88-Mar89	.264	1.322	.186		-.066	- .332	.740	
Apr88-Apr89	.117	.581	.575		.612	2.937	<0.01	**
May88-May89	.310	1.485	.138		.566	2.712	<0.01	**
June88-June89	.465	2.231	<0.05	*	.572	2.745	<0.01	**
Jan-Feb88	.512	2.558	<0.05	*	.228	1.141	.254	
Jan-Mar88	.397	1.985	<0.05	*	.341	1.707	.088	
Jan-Apr88	.199	.996	.319		.575	2.875	<0.01	**
Jan-May88	-.021	- .103	.918		.392	1.958	.050	
Jan-June88	.069	.343	.732		.371	1.855	.064	
Jan-July88	.316	1.578	.115		.046	.228	.820	
Jan-Aug88	.361	1.803	.072		.208	1.039	.299	
Jan-Oct88	.010	.048	.962		.438	2.192	<0.05	*
Jan-Nov88	.320	1.600	.110		.348	1.738	.082	
Jan-Dec88	.558	2.792	<0.01	**	.203	1.017	.309	
Feb-Mar88	.070	.348	.728		.289	1.444	.149	
Feb-Apr88	.065	.325	.745		.236	1.179	.239	
Feb-May88	.111	.553	.580		.519	2.594	<0.01	**
Feb-June88	.255	1.273	.203		.382	1.911	.056	
Feb-July88	.265	1.326	.185		.440	2.201	<0.05	*
Feb-Aug88	.396	1.981	<0.05	*	.355	1.774	.076	
Feb-Oct88	.143	.713	.476		.425	2.126	<0.05	*
Feb-Nov88	.501	2.503	<0.05	*	.502	2.511	<0.05	*
Feb-Dec88	.637	3.187	<0.01	**	.370	1.848	.065	
Mar-Apr88	-.167	- .834	.405		.205	1.027	.305	
Mar-May88	-.203	-1.015	.310		.150	.750	.453	
Mar-June88	-.441	-2.203	<0.05	*	.184	.918	.359	

	NEAR				FAR			
Months	r_s	Z	p		r_s	Z	p	
Mar-July88	-.018	- .091	.928		.134	.669	.503	
Mar-Aug88	.177	.883	.377		-.152	- .761	.447	
Mar-Oct88	-.002	- .012	.990		-.162	- .810	.418	
Mar-Nov88	.079	.396	.692		-.104	- .521	.603	
Mar-Dec88	.339	1.697	.090		-.023	- .117	.907	
Apr-May88	.490	2.450	<0.05	*	.080	.399	.690	
Apr-June88	.071	.356	.722		.363	1.816	.069	
Apr-July88	.323	1.615	.106		.015	.074	.941	
Apr-Aug88	.231	1.154	.249		.481	2.406	<0.05	*
Apr-Oct88	.086	.432	.666		.536	2.678	<0.01	**
Apr-Nov88	-.157	- .787	.431		.590	2.931	<0.01	**
Apr-Dec88	.056	.279	.780		.718	3.59	<0.001	***
May-June88	.401	2.007	<0.05	*	.631	3.157	<0.01	**
May-July88	.320	1.602	.109		.601	3.003	<0.01	**
May-Aug88	.140	.702	.483		.372	1.861	.063	
May-Oct88	.374	1.874	.061		.471	2.354	<0.05	*
May-Nov88	-.009	- .047	.963		.333	1.666	.096	
May-Dec88	.122	.608	.543		.178	.890	.374	
June-July88	.497	2.487	<0.05	*	.626	3.131	<0.01	**
June-Aug88	.341	1.703	.089		.491	2.456	<0.05	*
June-Oct88	.226	1.131	.258		.569	2.845	<0.01	**
June-Nov88	.147	.737	.461		.408	2.039	<0.05	*
June-Dec88	.343	1.716	.086		.450	2.250	<0.05	*
July-Aug88	.736	3.680	<0.001	***	.558	2.789	<0.01	**
July-Oct88	.491	2.456	<0.05	*	.360	1.800	.072	
July-Nov88	.221	1.105	.269		.339	1.693	.091	
July-Dec88	.313	1.567	.117		.320	1.602	.109	
Aug-Oct88	.371	1.854	.064		.629	3.143	<0.01	**
Aug-Nov88	.316	1.582	.114		.760	3.799	<0.001	***
Aug-Dec88	.543	2.716	<0.01	**	.741	3.703	<0.001	***
Oct-Nov88	.556	2.778	<0.01	**	.874	4.372	<0.001	***
Oct-Dec88	.259	1.297	.195		.726	3.630	<0.001	***
Nov-Dec88	.533	2.664	<0.01	**	.838	4.192	<0.001	***

Table 3.5.b: Friedman's Test Statistics for Monthly Proximity Distributions (df=3). A significant result indicates that the distribution of ranks over all months is different for the four distance categories. The ordering of distances is given, such that the significant result applies to the whole set and not to any two distance categories (the order reflects the ranking of the distance measures).

Name	χ_r^2	p	
Trossachs	46.839	<0.001 ***	(1-5>30-1>to 30>C)
Katrina	16.445	<0.001 ***	(1-5>30-1>C>to 30
Becky	28.145	<0.001 ***	(1-5>30-1>to 30>C)
Tessa	24.107	<0.001 ***	(1-5>30-1>to 30>C)
Pansy	21.426	<0.001 ***	(1-5>30-1>to 30>C)
Poppy	9.696	<0.05 *	(1-5>30-1>to 30>C)
Zac	39.497	<0.001 ***	(1-5>30-1>to 30>C)
Jenny	26.196	<0.001 ***	(1-5>30-1>C>to 30)
Calico	13.063	<0.01 **	(1-5>C>30-1>to 30)
Wanda	32.467	<0.001 ***	(1-5>30-1>C>to 30)
Laura	27.000	<0.001 ***	(1-5>30-1>C>to 30)
Molly	31.839	<0.001 ***	(1-5>30-1>to 30>C)
Daisy	42.745	<0.001 ***	(1-5>30-1>to 30>C)

(N.B. 1-5 = 1-5 metres, 30-1 = 30 centimetres-1 metre, to 30 = Less than 30 centimetres, and C = Contact)

Table 3.5.c: Individual Proximity Ranks Across All Months. A significant result means that the distribution of ranks over all months is different for the thirteen individual Adult cats. The ordering, by rank, of cats is given as a rough indicator of differences, but the significant result applies only to the entire set and not to comparisons between individuals.

Contact: df= 12, χ_r^2= 76.366, p<0.001

Jenny>Calico>Laura>Katrina>Wanda>Poppy>Zac>Becky/Tessa>Molly>Pansy>Trossachs>Daisy

Less than Thirty Centimetres: df= 12, χ_r^2= 33.951, p<0.001

Poppy>Jenny>Katrina>Tessa>Molly>Wanda>Zac>Pansy>Becky>Calico>Trossachs>Laura>Daisy

Thirty Centimetres to One Metre: df= 12, χ_r^2= 41.424, p<0.001

Jenny>Molly>Tessa>Wanda>Zac>Laura>Trossachs>Becky>Poppy>Katrina>Calico>Pansy>Daisy

One to Five Metres: df= 12, χ_r^2= 52.262, p<0.001

Zac>Jenny>Trossachs>Molly>Wanda/Laura>Tessa>Becky>Daisy>Katrina>Poppy>Calico>Pansy

Table 3.5.d: Proximity Differences Between Months (n= 13,13), Using a Mann-Whitney U-test to Compare "Near" and "Far" Distance Categories. A significant result indicates that individual cats had relatively constant ranks for Near and Far. Where the probability was non-significant, the usual explanation was high Near scores and very low Far scores due to huddling in shelters during cold or wet weather.

Month	**U**	**Z**	**p**
January 1988	64	-1.051	.293
February 1988	80.5	- .205	.837
March 1988	65	-1.001	.317
April 1988	6	-4.039	<0.001 ***
May 1988	13	-3.671	<0.001 ***
June 1988	0	-4.333	<0.001 ***
July 1988	4	-4.130	<0.001 ***
August 1988	0	-4.339	<0.001 ***
October 1988	9	-3.874	<0.001 ***
November 1988	5	-4.078	<0.001 ***
December 1988	16	-3.515	<0.001 ***
January 1989	2.5	-4.207	<0.001 ***
February 1989	9	-3.872	<0.001 ***
March 1989	5	-4.078	<0.001 ***
April 1989	52	-1.155	.248
May 1989	0	-4.158	<0.001 ***
June 1989	12	-3.475	<0.001 ***

Table 3.5.e: Correlations Between Seasons for Proximity Scores. Testing was performed as for Table 3.5.a, using reproductive seasons in place of months, and should be interpreted in the same way. Again, careful interpretation of significance levels is required with so many correlations.

		Near				Mid			
Seasons	**n**	**r_s**	**Z**	**p**		**r_s**	**Z**	**p**	
G1-B1	123	.469	5.177	<0.001	***	.618	6.825	<0.001	***
G1-G2	54	.584	4.255	<0.001	***	.698	5.080	<0.001	***
G1-B2	39	.277	1.705	.088		.542	3.340	<0.001	***
G1-W	123	.427	4.713	<0.001	***	.670	7.397	<0.001	***
G1-G1'	96	.347	3.379	<0.001	***	.559	5.446	<0.001	***
G1-B1'	96	.018	.178	.859		.039	.385	.701	
G1-G2'	66	.342	2.754	<0.01	**	.156	1.261	.207	
B1-G2	54	.107	.782	.434		.343	2.495	<0.05	*
B1-B2	39	.064	.397	.691		-.018	- .112	.911	
B1-W	69	.504	4.153	<0.001	***	.755	6.228	<0.001	***
	123	.163	1.801	.072		.567	6.262	<0.001	***
B1-G1'	96	.336	3.279	<0.001	***	.418	4.075	<0.001	***
B1-B1'	96	.255	2.484	<0.05	*	.210	2.044	<0.05	*
B1-G2'	66	.224	1.803	.071		.161	1.297	.195	
G2-B2	39	.314	1.934	.053		.613	3.780	<0.001	***
G2-W	54	.140	1.018	.309		.697	5.077	<0.001	***
G2-G1'	54	.427	3.111	<0.01	**	.587	4.275	<0.001	***
G2-B1'	54	-.125	- .909	.364		-.044	- .319	.750	
G2-G2'	54	.387	2.818	<0.01	**	.158	1.151	.250	
B2-W	39	-.036	- .222	.824		.534	3.293	<0.001	***
B2-G1'	39	.268	1.650	.099		.395	2.434	<0.05	*
B2-B1'	39	-.023	- .143	.886		-.153	- .946	.344	
B2-G2'	39	.137	.846	.398		.040	.248	.804	
W-G1'	115	.273	2.916	<0.01	**	.546	5.829	<0.001	***
W-B1'	115	.188	2.005	<0.05	*	.194	2.074	<0.05	*
W-G2'	66	.187	1.505	.132		.184	1.487	.137	
G1'-B1'	115	.297	3.175	<0.01	**	.029	.314	.753	
G1'-G2'	66	.621	5.009	<0.001	***	.377	3.037	<0.01	**
B1'-G2'	66	.405	3.269	<0.01	**	.091	.732	.464	

Far

Seasons	n	r_s	Z	p	
G1-B1	123	.581	6.414	<0.001	***
G1-G2	54	.679	4.946	<0.001	***
G1-B2	39	.515	3.174	<0.01	**
G1-W	123	.613	6.767	<0.001	***
G1-G1'	96	.634	6.180	<0.001	***
G1-B1'	96	.155	1.507	.132	
G1-G2'	66	.271	2.185	<0.05	*
B1-G2	54	.507	3.693	<0.001	***
B1-B2	39	.467	2.877	<0.01	**
B1-W	69	.764	6.304	<0.001	***
	123	.588	6.491	<0.001	***
B1-G1'	96	.528	5.149	<0.001	***
B1-B1'	96	.147	1.430	.153	
B1-G2'	66	.156	1.260	.208	
G2-B2	39	.453	2.795	<0.01	**
G2-W	54	.657	4.785	<0.001	***
G2-G1'	54	.693	5.043	<0.001	***
G2-B1'	54	-.079	- .577	.564	
G2-G2'	54	.329	2.393	<0.05	*
B2-W	39	.352	2.167	<0.05	*
B2-G1'	39	.465	2.869	<0.01	**
B2-B1'	39	.006	.037	.970	
B2-G2'	39	.278	1.711	.087	
W-G1'	115	.680	7.258	<0.001	***
W-B1'	115	.533	5.695	<0.001	***
W-G2'	66	.244	1.970	<0.05	*
G1'-B1'	115	.467	4.989	<0.001	***
G1'-G2'	66	.281	2.266	<0.05	*
B1'-G2'	66	.197	1.584	.113	

Table 3.5.f: Individual Effect on Seasonal Scores, Using a Kruskal-Wallis Test. Significant values indicate differences among the individual cats tested over a given season and distance category. Note that breeding Females differ (in proximity to other cats) among themselves to the greatest degree in the Breeding and Winter seasons, while other cats show differences (in proximity to breeding Females) throughout the year.

Season	Distance	df	n	H	p
FEMALES TO ALL OTHERS					
$Gestation_1$	Near	8	123	8.619	.375
$Gestation_1$	Mid	8	123	8.758	.363
$Gestation_1$	Far	8	123	18.869	<0.05 *
$Breeding_1$	Near	8	123	26.931	<0.001 **
$Breeding_1$	Mid	8	123	19.344	<0.05 *
$Breeding_1$	Far	8	123	26.994	<0.001 ***
$Gestation_2$	Near	3	54	4.576	.206
$Gestation_2$	Mid	3	54	6.214	.102
$Gestation_2$	Far	3	54	4.090	.252
$Breeding_2$	Near	2	39	11.036	<0.01 **
$Breeding_2$	Mid	2	39	3.407	.182
$Breeding_2$	Far	2	39	1.335	.513
Winter	Near	11	142	46.192	<0.001 ***
Winter	Mid	11	142	27.259	<0.01 **
Winter	Far	11	142	22.444	<0.05 *
$Gestation_1'$	Near	9	115	8.315	.503
$Gestation_1'$	Mid	9	115	10.477	.313
$Gestation_1'$	Far	9	115	18.200	<0.05 *
$Breeding_1'$	Near	9	115	20.763	<0.05 *
$Breeding_1'$	Mid	9	115	62.947	<0.001 ***
$Breeding_1'$	Far	9	115	56.875	<0.001 ***
$Gestation_2'$	Near	4	66	2.558	.634
$Gestation_2'$	Mid	4	66	3.915	.418
$Gestation_2'$	Far	4	66	5.502	.240

Season	Distance	df	n	H	p
OTHERS TO BREEDING FEMALES					
$Gestation_1$	Near	28	123	69.825	<0.001 ***
$Gestation_1$	Mid	28	123	95.159	<0.001 ***
$Gestation_1$	Far	28	123	94.986	<0.001 ***
$Breeding_1$	Near	28	123	75.604	<0.001 ***
$Breeding_1$	Mid	28	123	82.971	<0.001 ***
$Breeding_1$	Far	28	123	78.616	<0.001 ***
$Gestation_2$	Near	28	54	43.959	<0.05 *
$Gestation_2$	Mid	28	54	44.441	<0.05 *
$Gestation_2$	Far	28	54	45.921	<0.05 *
$Breeding_2$	Near	27	39	23.995	.631
$Breeding_2$	Mid	27	39	30.943	.274
$Breeding_2$	Far	27	39	34.322	.157
Winter	Near	28	142	40.424	.061
Winter	Mid	28	142	89.477	<0.001 ***
Winter	Far	28	142	102.494	<0.001 ***
$Gestation_1'$	Near	28	115	48.837	<0.01 **
$Gestation_1'$	Mid	28	115	62.939	<0.001 ***
$Gestation_1'$	Far	28	115	87.911	<0.001 ***
$Breeding_1'$	Near	28	115	57.904	<0.001 ***
$Breeding_1'$	Mid	28	115	33.047	.234
$Breeding_1'$	Far	28	115	50.972	<0.01 **
$Gestation_2'$	Near	28	66	52.071	<0.01 **
$Gestation_2'$	Mid	28	66	48.781	<0.01 **
$Gestation_2'$	Far	28	66	48.482	<0.01 **

Table 3.5.g: Individual Correlations Between Reproductive Seasons. A significant result means that, for any individual breeding Female, the two seasons are linearly correlated over the proximity category. For example, the ranks for Becky's Near proximity to other cats are positively correlated for $Gestation_1$ and $Breeding_1$. Again, careful interpretation of significance levels is required with so many correlations.

(*= $p<0.05$, **= $p<0.01$, ***= $p<0.001$)

("-" indicates negative correlations, all others are positive correlations)

NEAR	Katrina	Becky	Tessa	Poppy	Bojangles	Pippin	Jenny	Calico	Wanda	Molly	Daisy	Mulberry
G1-B1		*	*				*	*	*	***	*	
G1-G2							**	**				
G1-B2							*					
G1-W		*					*		*	**		
G1-G1'								*				
G1-B1'					-*						*	
G1-G2'								*				
B1-G2							*	*				
B1-B2							**					
B1-W									**	**	*	
B1-G1'				*	*							
B1-B1'							***			*		
B1-G2'								*				
G2-B2							**					
G2-W				-*			*					
G2-G1'								*	*			
G2-B1'									-*			
G2-G2'								*				
B2-W												
B2-G1'								**				
B2-B1'												
B2-G2'								**				
W-G1'							*		*			
W-B1'								*		*		
W-G2'			*				*					
G1'-B1'	*		*									
G1'-G2'	**						**					
B1'-G2'	**											

MID	Katrina	Becky	Tessa	Poppy	Bojangles	Pippin	Jenny	Calico	Wanda	Molly	Daisy	Mulberry
G1-B1	*	**	*	*				*	***	**	*	
G1-G2			*	*			**	***				
G1-B2			**				*					
G1-W	*	**	**				**		**	**	*	
G1-G1'			*				**		*	**		
G1-B1'							*			*		
G1-G2'												
B1-G2			**	*				**				
B1-B2			**									
B1-W	**	**	*					*	**	***	**	
B1-G1'			**					*	*	**		
B1-B1'							***					
B1-G2'												
G2-B2			*				*					
G2-W							**	*				
G2-G1'			*				*					
G2-B1'												
G2-G2'												
B2-W			*				*					
B2-G1'			*				**					
B2-B1'							*					
B2-G2'												
W-G1'		*	*				*		**	*		
W-B1'						*						
W-G2'							*					
G1'-B1'							*					
G1'-G2'												
B1'-G2'							*					

FAR	Katrina	Becky	Tessa	Poppy	Bojangles	Pippin	Jenny	Calico	Wanda	Molly	Daisy	Mulberry
G1-B1	*	**	**	*			*		**	**	*	
G1-G2			*	*			**					
G1-B2			*									
G1-W	**	*		**			*		**	**	**	
G1-G1'		*	**				**	*	*	*		
G1-B1'										*		
G1-G2'								*				
B1-G2			*	*				***				
B1-B2							*					
B1-W	**	**		**				**	***	*	**	
B1-G1'		**	*	*				**	**	*		
B1-B1'							*			*		
B1-G2'												
G2-B2												
G2-W			*	*			**	**				
G2-G1'							**	**				
G2-B1'												
G2-G2'												
B2-W												
B2-G1'			*									
B2-B1'												
B2-G2'												
W-G1'		*		**			***	*	**	**		
W-B1'							*		*	*		*
W-G2'							**	*				
G1'-B1'							**		**	*		*
G1'-G2'							*					
B1'-G2'		**										

for close distances were found in the winter months (January to March) and the communal breeding period (April to July) of the two years, although the warmer winter of 1989 gave low ranks to the early months of that year. The high ranks for greater distances were scattered throughout 1988 and 1989. As before, rank orders are provided only as indicators of the extremes, and not as statistically different entities (except as tested in a complete set).

When the monthly distribution of proximity scores was examined more closely, using all distance measures, few differences from the overall totals were found, such that most individuals showed a significant diversity of values between distances. All cats had more One to Five Metre observations, followed by Thirty Centimetres to One Metre observations, except Calico; some Females also had more Contact measures than Less than Thirty Centimetres (e.g. Katrina, Jenny, Wanda and Laura), but scores generally decreased with decreasing distances (Table 3.5.b). Individuals were then compared for each proximity total, to the effect that Jenny always had a high rank ranging down to Pansy and Daisy, who always had low ones. It is possible that this represents a spectrum from "Central" to "Peripheral" animals (Table 3.5.c), with most cats falling in the middle of the range, depending on the distance sampled. The two "Near" values were then lumped, as were the "Far" measures; all individuals, bar Calico ($p = .653$), spent significantly more time being scanned at greater distances from a larger number of other individuals. This was also true for each separate month, except those with high scores for close proximity (Table 3.5.d). Generally, it would seem that there may have been an effect of reproductive season, and so this possibility was examined, with breeding Females as the criteria for the divisions into periods.

Three different distance categories were used for the analysis of seasons, in order to maximise the possibility of detecting changes at any range: "Near" again corresponded to Contact plus Less than Thirty Centimetres; "Mid" equalled Thirty Centimetres to One Metre; and "Far" was One to Five Metres only. Over all Females, associations were found between the proximity scores for similar reproductive states such as Breeding and Gestation; this effect was not as clear for each individual Female, and only Gestation periods seemed consistently correlated. A complicating feature was the different pattern of reproduction for individuals, with only some of the Females breeding at any one time. In fact, the second Breeding season of 1988 was not apparently affiliated to the other two possible Breeding periods. Sequential seasons were also correlated to some extent, while few links were seen between unlike, non-sequential periods. The full panoply of Spearman Correlation statistics is presented in Table 3.5.e.

The correlation results suggest that "Near" proximity was more sensitive to seasonal changes, "Mid" was less so, and "Far" was generally linked over all periods.

"Near" associations had explicable causes relating to different sets of relationships, while "Mid" and "Far" correlations were found between apparently reproductively unconnected groups. Only closer distances were examined for details, as the greater ranges appeared to reflect less specific associations, and tended toward random connections due to consistent levels for seasonal measures. At close proximity, Winter was numerically affiliated to the following Breeding season, although not the second one; and was in turn related to the preceding spring Gestation and spring Breeding (and again, not to the second set of the year). Gestation periods were themselves inter-related, both within years and between them, as well as to the subsequent Breeding seasons. Breeding was also somehow connected between years, but not within the same year. Non-consecutive, non-similar seasons were not significantly correlated, with the exception of $Breeding_1$ and $Gestation_1'$, which were both linked to Winter as well (Figure 3.8.a).

From this set of relationships, it is possible that the basic reproductive year follows the order - Winter, Gestation, Breeding, Winter - with more-or-less consistent proximity associations, perhaps aided by the phenomenon of birth synchrony. When two litters (or more) were born in one year, which was not wholly uncommon, the lack of synchrony later in the year may have affected otherwise stable relationships; with less cooperative care, perhaps fewer close pairings were seen in proximity scans. Intimate proximity relationships may prove to be predictive from one spring to the next (Gestation and Breeding), but not from spring to summer reproduction, or summer to summer between years (although Gestation was linked, and so perhaps, with completed samples, Breeding would also have been related).

Individual Focal Females had a significant effect on the values for each season, especially Breeding and Winter at all distances (Table 3.5.f); Wanda and Molly were highest ranked for $Breeding_1$, Calico, Molly Jenny and Wanda for Winter, and Wanda and Molly again for $Breeding_2$. The non-Focal "recipients" also had an effect on seasonal proximity scores (Table 3.5.f) over most seasons; at close and middle ranges, Zac, Jenny and Laura were highest ranked, while Zac, Trossachs, Jenny and Laura led the field at greater distances.

The last seasonal aspects to be considered were the individual patterns of relationships over the seasons for each Female and their preferred partners for each period. Again, middle- and long-range scores showed more statistically significant combinations, while short distances had fewer seasonal connections; a summary of the correlations is given in Table 3.5.g, with significance levels only. Females showed associations within and between Gestation and Breeding seasons, with a Winter connection in Group B cats; Katrina had the basic pattern of Gestation, Breeding, Winter, as did Becky, Poppy and Daisy, and other cats had more connections between "like" seasons. Despite a certain

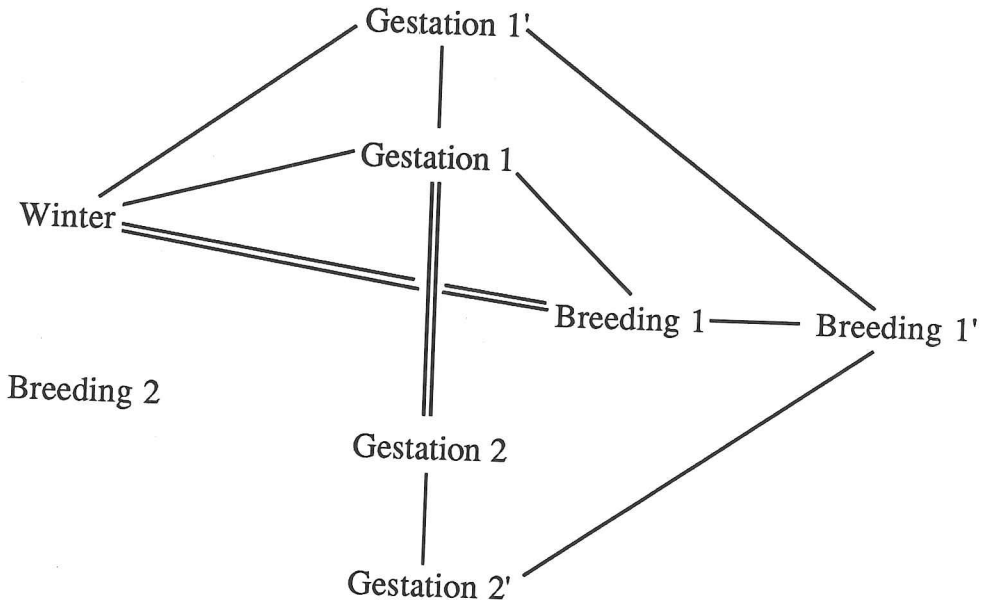


Figure 3.8.a: A summary of correlations between reproductive seasons over all breeding Females at "Near" distances (less than 30 centimetres). The statistics are given in Table 3.5.e. "1" marks the first litters of 1988, "2" marks the second litters of 1988, while "1'" and "2'" denote the first and second litters of 1989.

Figure 3.8.b

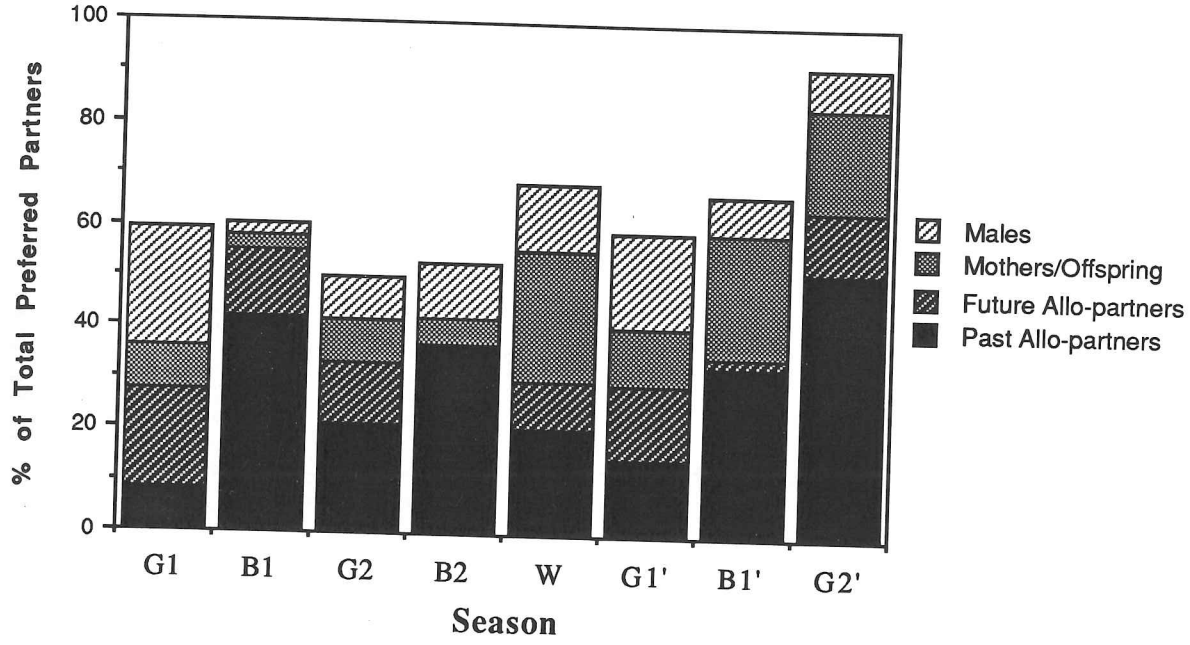


Figure 3.8.c

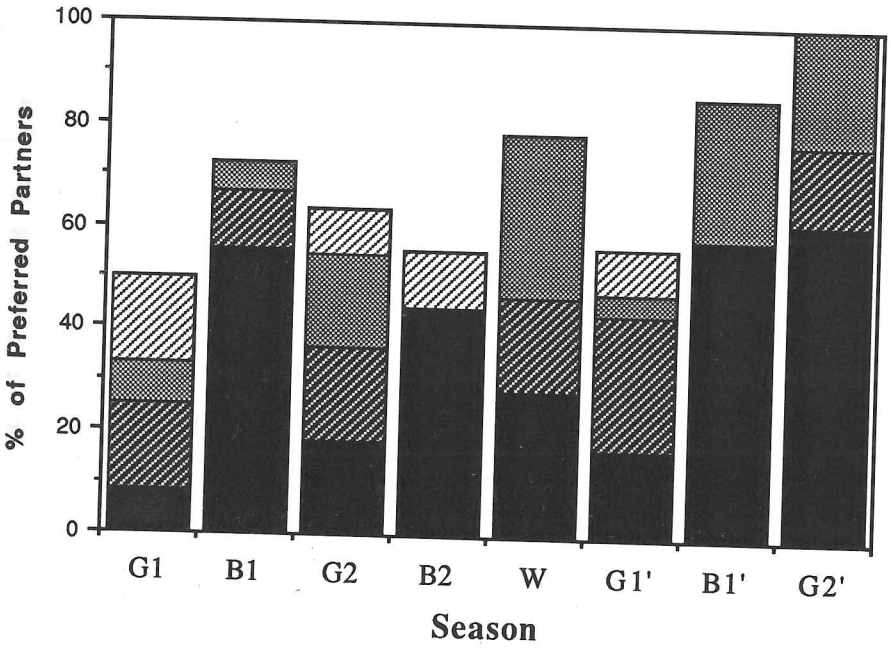


Figure 3.8: The "preferred" partners for each reproductive season and over all breeding Females. Partners correspond to the cat most often seen at a given distance from the Focal individual. (**b**) Over All Distances (to five metres); (**c**) Close Proximity (contact plus less than 30 centimetres).

Figure 3.8.d

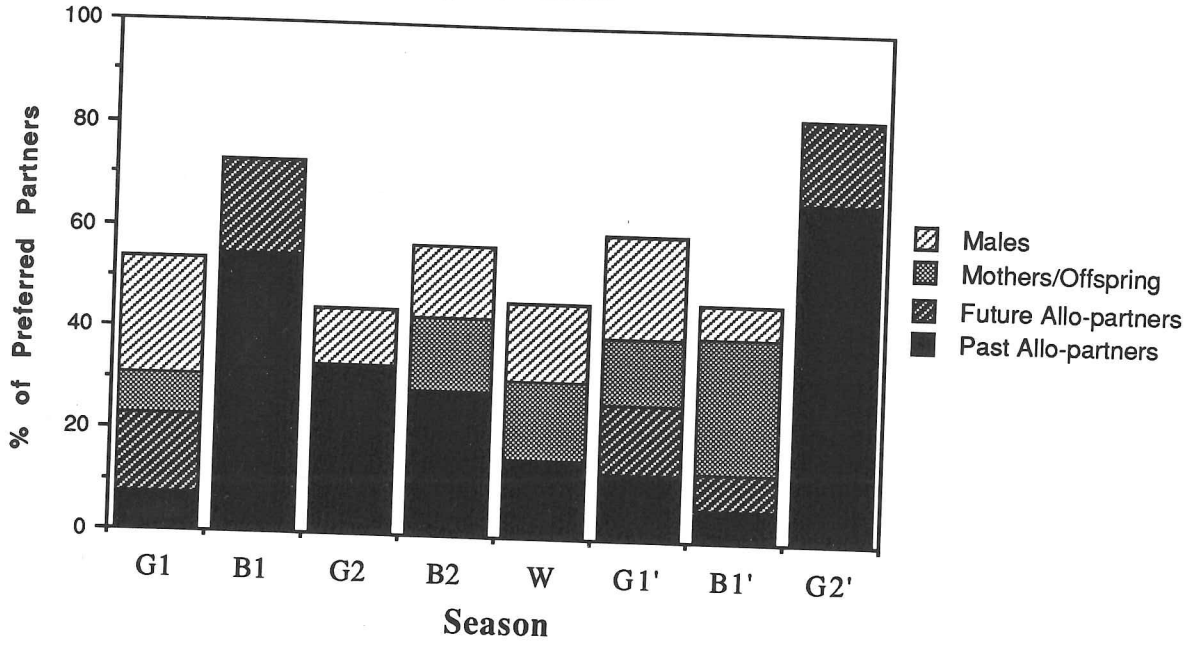


Figure 3.8.e

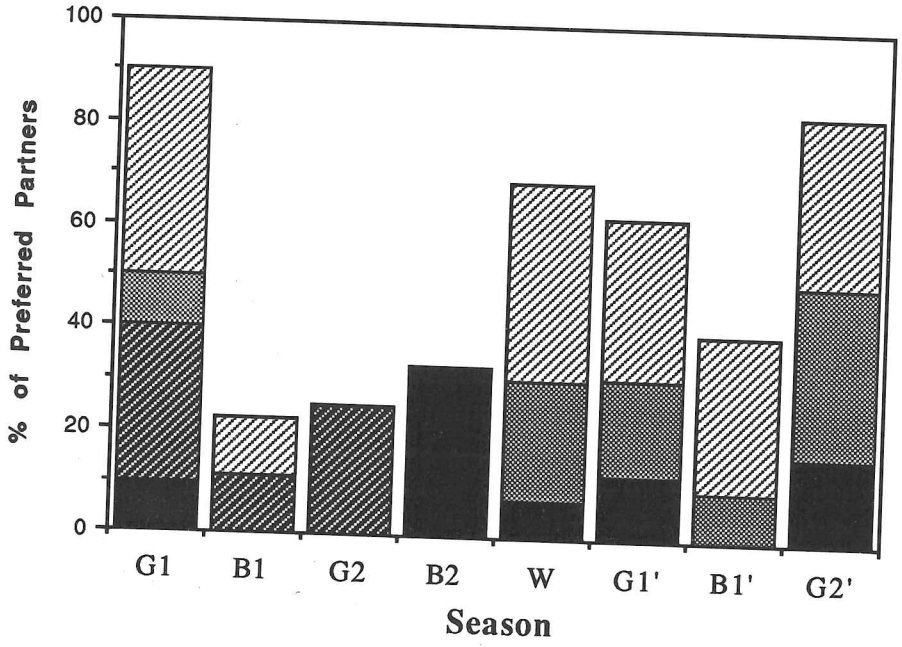


Figure 3.8: The "preferred" partners for each reproductive season and over all breeding Females. Partners correspond to the cat most often seen at a given distance from the Focal individual. (**d**) Middle Distance (thirty centimetres to one metre); (**e**) Long Distance (one to five metres).

scatter of correlations, the same underlying structure would seem to exist for individuals as well as overall.

A few negative correlations were found at close quarters, but these resulted from previously communal mothers becoming more solitary for second litters or subsequent years, and from changes in partners (e.g. Calico and Poppy). As for preferred partners, these showed a striking arrangement (Figure 3.8.b), such that, over all three distance categories, cooperative partners were most favoured, especially during Breeding and the subsequent Gestation, when Kittens were still present. Relatives (mothers or offspring) were particularly preferred in the Winter, and Males were often nearby in early Gestation (e.g. mating). Some differences were also seen at each distance (Figures 3.8.c-e). For each Female, the details of reproductive alliances affected the pattern of preference.

When only Contact was considered, Katrina spent most time with Pansy (who preferred Poppy) in Gestation; this choice gave way to Poppy for Breeding (they shared a litter which Katrina soon abandoned) and for the following Winter (despite the removal of any surviving joint offspring). Poppy mainly reciprocated these attentions, and also included a past "offspring", Bojangles, in the Winter; the following year, she again focussed on Katrina, who died suddenly, and Poppy was then seen primarily with Tessa and Tycho, who were co-helpers. A similar, but not identical, pattern was observed up to One Metre (excluding Contact), with the inclusion of Becky (a past partner for Poppy). Becky consistently preferred Tessa through the year, while Poppy played an increasing role in 1989, when she helped Becky with a litter (and later in 1989, when they pooled another batch of kittens); Tessa reciprocated, only including Poppy for the short period in which they were communal (a matter of days). Poppy was increasingly favoured at a slightly greater distance from both Becky and Tessa, such that these cats were often very closely affiliated, but not as often in Contact. The two younger cats, Bojangles and Pippin, were seen most at close ranges with their "mother", Poppy, over the Winter, and then showed no preference for an Adult as they bred together.

Similar anecdotes linked the cats in Group B. Jenny showed changing preferences with each season, no doubt associated with the other cat's activities and responses; Wanda was favoured during early Gestation and Breeding periods, while Laura and Molly were late summer and Winter partners. The Males, Zac and Dijon, were more involved at a slightly greater radius. Wanda, however, favoured Calico during Breeding both years, and spent Winter and Gestation with Jenny and Zac at closer distances. Calico reciprocated the attentions of Wanda, and included younger helpers during Winter and the next Breeding period, while she was also involved with Jenny in Gestation (an apparent cold-weather resting coalition). Molly also preferred Jenny, except when communal with Mulberry and Laura in 1989; these breeding cooperators were evident in the preceding year

as close (but not Contact) partners. Daisy, the more solitary Female, preferred Jenny and her son, Duffy, for Contact, but these values were strikingly low.

At middle distance, many of the same partners existed, but there seemed to be less association with reproductive units, and additional connection to other social pairings. Males were more prominently involved, as well as additional offspring; Becky, Tessa and Poppy again were inter-related, while Jenny and Molly showed strong preferences for one another (especially Molly favouring Jenny). Other Females had scattered inclinations, including the same allies found at close distance, as well as new ones; Jenny appeared in many combinations. At the greatest distance, Males were almost the sole preferred partners for all Females; some other partners were indicated, but they were mainly swamped by the increased presence of Adult Males.

The next section will investigate the influence of weather on proximity observations, as one possible factor affecting the associations that were seen.

3.5.3. WEATHER

As prefaced in Chapter 2, monthly statistics were obtained to allow comparisons between proximity relationships and weather conditions. To begin with, individual cats were compared for their monthly values in Contact with other animals; a few significant negative correlations were found, such that Contact was associated with Mean Maximum Temperature for Poppy ($p<0.01$), Jenny and Calico ($p<0.05$) only, Mean Minimum Temperature for Trossachs, Katrina and Poppy ($p<0.05$), and Sunshine for Jenny and Calico ($p<0.05$). As Maximum and Minimum Temperature were strongly correlated to one another and to Sunshine (Section 2.4.6), it was impossible to tell which variable was responsible for the association; however, the general gist was that colder weather (with decreased sunshine) corresponded to increases in Contact levels for the five individuals mentioned.

Individuals were again tested for correlations between weather and proximity, using lumped measures for "Near" (less than 30 centimetres) and "Far" (30 centimetres to 5 metres). The "Near" values showed few associations, as before; Maximum and Minimum Temperature were negatively correlated in Pansy (Maximum: $r_S= .525$, $Z= -2.101$, $p<0.05$, $n= 17$; Minimum: $r_S= -.572$, $Z= -2.287$, $p<0.05$, $n= 17$) and in Poppy (Maximum: $r_S= -.690$, $Z= -2.761$, $p<0.01$, $n= 17$; Minimum: $r_S= -.612$, $Z= -2.448$, $p<0.05$, $n= 17$), who were commonly in the same shelter in the cold months of late winter, and Molly increased her Contacts as Sunshine increased ($r_S= .537$, $Z= 2.147$, $p<0.05$, $n= 17$), perhaps due to the fact that groups of cats rested together in small patches of sunlight, or in the shade during particularly hot weather. At "Far" distances, more correlations were found (Table 3.6); in general, increased temperatures

Table 3.6: Correlations of Individual Proximity at Long Distance With Weather Variables. Significant probability levels mean that, for a given individual cat, the ranks of the proximity scores (1-5 metres) over all months are linearly related to the ranks of the weather variable over those months.

Name	Weather	n	r_s	Z	p	
Trossachs	Max. Temp.	17	.477	1.909	.056	
Trossachs	Min. Temp.	17	.540	2.160	<0.05	*
Trossachs	Hrs of Sun	17	.234	.937	.349	
Trossachs	Rainfall	17	-.128	- .510	.610	
Katrina	Max. Temp.	14	.675	2.435	<0.05	*
Katrina	Min. Temp.	14	.691	2.491	<0.05	*
Katrina	Hrs of Sun	14	.332	1.197	.232	
Katrina	Rainfall	14	.231	.832	.405	
Becky	Max. Temp.	17	.406	1.624	.105	
Becky	Min. Temp.	17	.513	2.050	<0.05	*
Becky	Hrs of Sun	17	.108	.431	.666	
Becky	Rainfall	17	-.245	- .980	.327	
Tessa	Max. Temp.	17	.614	2.457	<0.05	*
Tessa	Min. Temp.	17	.721	2.884	<0.01	**
Tessa	Hrs of Sun	17	.279	1.118	.264	
Tessa	Rainfall	17	-.069	- .275	.784	
Pansy	Max. Temp.	17	.396	1.585	.113	
Pansy	Min. Temp.	17	.398	1.590	.112	
Pansy	Hrs of Sun	17	.195	.780	.436	
Pansy	Rainfall	17	-.537	-2.148	<0.05	*
Poppy	Max. Temp.	17	.776	3.105	<0.01	**
Poppy	Min. Temp.	17	.786	3.144	<0.01	**
Poppy	Hrs of Sun	17	.561	2.245	<0.05	*
Poppy	Rainfall	17	.012	.049	.961	

Name	Weather	n	r_s	Z	p	
Zac	Max. Temp.	17	.473	1.893	.058	
Zac	Min. Temp.	17	.573	2.291	<0.05	*
Zac	Hrs of Sun	17	.346	1.382	.167	
Zac	Rainfall	17	-.145	- .578	.563	
Jenny	Max. Temp.	17	.771	3.085	<0.01	**
Jenny	Min. Temp.	17	.796	3.183	<0.01	**
Jenny	Hrs of Sun	17	.596	2.382	<0.05	*
Jenny	Rainfall	17	.061	.245	.806	
Calico	Max. Temp.	17	.575	2.300	<0.05	*
Calico	Min. Temp.	17	.673	2.693	<0.01	**
Calico	Hrs of Sun	17	.485	1.941	.052	
Calico	Rainfall	17	-.027	- .108	.914	
Wanda	Max. Temp.	17	.769	3.075	<0.01	**
Wanda	Min. Temp.	17	.793	3.174	<0.01	**
Wanda	Hrs of Sun	17	.532	2.127	<0.05	*
Wanda	Rainfall	17	.091	.363	.717	
Laura	Max. Temp.	17	.413	1.653	.098	
Laura	Min. Temp.	17	.459	1.834	.067	
Laura	Hrs of Sun	17	.233	.931	.352	
Laura	Rainfall	17	-.108	- .431	.666	
Molly	Max. Temp.	17	.573	2.291	<0.05	*
Molly	Min. Temp.	17	.622	2.487	<0.05	*
Molly	Hrs of Sun	17	.488	1.951	.051	
Molly	Rainfall	17	-.125	- .500	.617	
Daisy	Max. Temp.	17	.533	2.134	<0.05	*
Daisy	Min. Temp.	17	.651	2.605	<0.01	**
Daisy	Hrs of Sun	17	.309	1.235	.217	
Daisy	Rainfall	17	.039	.157	.875	

(and occasionally sunshine) were associated with increases in distant measures for most individuals. This was undoubtedly a result of the greater levels of activity outside the shelters in all but the worst weather; only Pansy and Laura differed, the former because of her more solitary nature (she was rarely found in the general vicinity of social groups) and the latter because of her apparent preference for closer proximities to partners. Pansy was also the sole cat to significantly increase her proximity value in correspondence with decreases in rainfall; she presumably took cover vigourously and away from others, so that rainy months saw her in isolated shelter. Other cats seemed to take cover in communal areas and shelters, so that rain did not affect their scores.

In order to examine bigger trends than those for individuals, mean proximity scores were tested against the weather values. Some interesting differences were found between the two groups; the proximities of cats in Group A were significantly associated with temperature, such that values for "Near" increased in colder months (common shelters and huddling) while "Far" values increased in warmer months (more general activity and casual distances). Cats in Group B did not generally show any correlation between "Near" scores and weather, perhaps due to the balancing influence of warm weather resting partners; "Far" values were similar to those discussed for Group A. Altogether, closer proximities were not significantly correlated with weather, while more distant proximities increased in warm weather.

3.6. DISCUSSION

Many studies of behavioural ecology, and of cats in particular, have used proximity scans and preferred partner data to describe many aspects of social organisation (Dards 1979; Liberg 1981; Kerby 1987). However, from the present study, it seems apparent that the choice of distance limits strongly affects the type of relationships sampled; contact and other intimate ranges appeared, at least in this study, to reflect on-going reproductive concerns and some social coalitions, while middle distances echoed more general social relationships. Long-distance scans were less specific, and probably referred more to aspects such as mating and the use of common areas. One complication was the predominance, in numbers, of scores from greater distances, so that lumped data could only reflect any spatial interactions that were consistent over all distance ranges and those interactions from the longest distances. The details of social associations would be completely obscured by the pooling from different Focal radii, and nearest neighbours would reflect only the closest seasonal reproductive alliances. Therefore, it is important to

look at all of these factors separately to see if there is any one way to predict relationships from proximity scans.

Although the results of the proximity analysis showed a degree of scatter, some consistent associations were found. No overall differences were found between the two groups with respect to spatial relationships for Adults. Proximity relationships up to five metres were non-random, and each individual had common partners at different levels. Males were scanned most at longer distances from all others, and showed a particular aversity to other Males at any close range. Females favoured the company of other Females, both Adult and Juvenile, for short distances (see Dards 1979), while Males were most common at longer ones. A linear association was found for measures of the two closer distances based on individual Adult totals (Contact and Less than Thirty Centimetres), as well as for the two greater extents (Thirty Centimetres to One Metre and One to Five Metres); this allowed the pooling of data into two categories, "Near" and "Far", to facilitate some comparisons. Differences in Adult Male and Female distances were seen for certain pairings of individuals; it is possible that the closest Females were those with stable social relationships with the Males, and those found farther away (the most often) were the objects of sexual interest; in that case, Trossachs and Katrina or Poppy, Zac and Wanda might be amicable combinations, while Trossachs and Tessa, plus Zac and Jenny might be reproductive sets, or just indicators of two core cats (as Males were often in the central feeding area). Juvenile and Kitten scores displayed small disparities between the two cat groups, probably due to the different sex-compositions of the groups. The difference between close and distant proximity between Adults and others may well reflect the varying nature of relationships, in that remaining close to others involved active approach and the absence of withdrawal, while distances as large as four or five metres could be maintained without much apparent notice of the others in this range. For this reason, Approach as a Focal behaviour was defined as the directed initiation of a proximity of less than one metre; behavioural aspects will be fully discussed in Chapter 4.

Juveniles tended to remain closer to one another until they were Adults, but were also affiliated to Females (as in Dards 1979); certain Juveniles had more potentially affiliative relationships with Adults, as indicated by the maintenance of closer proximity. This corresponds, in part, to the differences between Males and Females in their social dynamics, as well as to individual differences. Juvenile Males appeared to refrain from feeding with the other cats, but often crept (literally) in later, after Adults had finished eating and dispersed; feeding seemed the major reason for visiting the core area in the absence of closer social bonds with the other cats. It is possible that kinship and familiarity influence closer proximity relationships (Berman 1983a), which in turn might be passively boosted by inter-Adult alliances; offspring may show close proximity relationships with mothers and with mothers' "partners" in turn.

It would appear that younger Juvenile Males (e.g. those born in 1988 in this study) had relatively amicable relations with the Adult Male, and were found in the same area, along with various Females; as Males matured, they tended to spend less time in the core area, and were usually seen at some distance from the Adult Male (as well as from other Adults). Increasing conflict between "competing" Males may account for this change in spatial relations. Adults appeared to have several factors influencing their proximity relationships with Juveniles; these included early experience such as mothering or allomothering, inter-Male conflict and individual differences in interactions (e.g. cats who seemed more solitary or social, either avoiding or initiating closer proximities with certain others). In summary, Adult-Juvenile proximity seemed to be affected by early rearing experience of mothers and allomothers or "aunts", as well as by inter-Male aggression and individual differences.

Overall proximity scores and the differences between individuals (Section 3.4.1) hinted at the presence of "Central" Females (e.g. Jenny, and perhaps Poppy, Tessa or Molly) and "Peripheral" or solitary ones (e.g. Daisy), as in Dards (1979) and Kerby (1987). The distinctions were less clear than in these other studies, and only cats at either end of the continuum could be distinguished. Females also varied as to the time scanned with young Kittens, and discrepancies might have arisen from differences in maternal interest, separating "good" attentive Females from "poor" unmindful ones. The first group of Females spent large amounts of time with Kittens, both their own and those of other mothers; they might correspond to genuinely cooperative Females. The second group were seen only with their own offspring, and may tend to be solitary Females (they may also lack the numerical strength of a combined communal litter), and the third group of Females, who appeared to "prefer" the company of other Kittens to their own might be indicative of "poor" mothers, who either abandon their own offspring or yield up the burden of care to more constant Females.

In summary, the general analysis of the proximity relationships in this study showed the following results: the two groups differed little in terms of spatial measures; spatial relations were not random, and both age and sex class influenced these interactions; Females appeared to be particularly important when considering close-proximity associations and other affiliations; Juvenile proximity may have been affected by early experience of Females (e.g. mothers and "aunts"), as well as by the relationships based on reaching sexual maturity; Female proximity to Kittens may have reflected maternal attentiveness to young offspring; all cats showed differences in their partner preferences; and individuals differed greatly in their proximity relationships, perhaps hinting at a continuum from "Central" to "Peripheral" animals. Once the basic questions were asked about the organisation of the framework underlying the social structure of this particular

population, a more specific investigation was undertaken. The guiding queries for the remainder of the chapter were as follows: "could proximity relationships be predicted from one season to the next?", "were cooperative partners distinguishable before the birth of litters?", and "were Solitary and Communal Females distinguishable outside the breeding season?"

Weather analysis (Section 3.5.3) suggested several patterns. Colder temperatures were associated with increased Contact for some individuals; this was probably due to the observed tendency for resting in the wooden shelters in groups of two or more cats during the cold winter months (strongly evinced by Poppy with Katrina and by Jenny, Calico and a group of younger cats). Overall, some trends relating weather and proximity could be observed, such that winter and summer appeared to have slightly different sets of proximity relationships. In the winter, some cats tended to huddle together more; the majority, however, may have countered any winter huddling with group summer sunbathing. On the other hand, the cats generally moved around within five metres of one another in the summer, perhaps using similar areas or nearby paths; in better weather, fewer cats were isolated in sheltered areas, and there were increased opportunities for chance "encounters".

Generally, Females seemed to prefer the company of their reproductive partners and helpers. When the data were divided into months of the year, correlations and other tests indicated groups which roughly corresponded to changes in weather and reproductive state. Therefore, seasons were defined for each reproductive Female, and used as the foundation for further analysis. As with the complete data, strong relationships were found between consecutive seasons, giving a cycle of Winter to Gestation to Breeding to Winter, so that only spring reproduction fit securely into the proposed circular structure. Across years, similar reproductive periods were also related, especially for Gestation, which might have slightly overlapped with Winter; within years, different Gestation periods were again associated.

Based on the observed trends connecting Winter with spring Gestation and spring Breeding, creating a cyclical pattern founded on reproductive states, a possible mechanism is suggested. It would appear that close relationships were reinforced by the resting coalitions who remained together in cold weather, mainly Winter; these then carried through to first Gestation, and birth synchrony allowed continuation through to Breeding, when the Females formed cooperative groups. Females who succeeded in rearing a spring litter were less likely to breed twice, and the birth synchrony of spring broke down as the failure of litters brought on oestrus. Later litters were not surrounded by the same proximity relationships, which did, however, resume in the Winter and the following year; seasonal preferred partners supported the general suggestion. One individual, Jenny,

appeared to hold a similar set of proximity relationships throughout the year, regardless of season; whether this was an outcome of her failure to care actively for kittens, or even a partial cause, she certainly was unique among the Females.

In answer to those questions posed earlier in the discussion, it appears that it would be possible to predict spatial relationships from season to season and from one year to the next, based on the reproductive state of the Focal Female. Cooperative partners were detected before the start of the relevant Breeding period, as given by the associations between proximity relationships in Gestation and Winter, as well as in Breeding seasons. Often, cooperative partners were also preferred proximity partners for distances less than 30 centimetres, both before and after the season in which they combined efforts in kitten-rearing. As for the third question, pertaining to the differences between Solitary and Communal Females, it seemed that Communal Females were generally more available (e.g. in sight and within five metres of another cat) than the Solitary and non-breeding Females. In addition, Communal Females showed more associations between close proximity relationships over the various reproductive seasons, while Solitary Females were less consistent. Unfortunately, the ability for each individual Female to shift between types of care (Solitary or Communal) complicated the relationships seen at any one time, and the overall paucity of Solitary Females also meant that these general associations require more investigation. However, the indications were quite strong, and must be qualified mainly because the sample sizes were relatively small.

The proposed scenario (in which close relationships were reinforced by the resting coalitions who remained together in cold weather, and carried through to first Gestation and Breeding, when the Females formed cooperative groups, and on into the Winter and the following year) could give rise to the results found in this study (a cycle of proximity correlations from Winter to Gestation to Breeding to Winter), and implies a stable set of associations between Females which might play a role in the maintenance of the group and breeding alliances. The possible behavioural mechanisms through which the society might coalesce are discussed in Chapter 4, and the details of reproduction and cooperation are presented in Chapter 5. All three of these features will be combined and integrated in the final part, Chapter 6.

Three adult females, Molly (left), Jenny (centre) and Laura (right), engaged in a complicated interaction of cheek and head rubbing, plus close sniffing (and licking: Jenny to Laura). (see Sections 2.3.2, 4.3.1 and 4.4.1)

Two adult females, Wanda (left) and Molly (right). Molly is body rubbing Wanda. Note the slightly arched posture. (see Sections 2.3.2 and 4.6)

Chapter 4

Focal Social Behaviour

4.1. GENERAL INTRODUCTION

4.1.1. PREFACE

Spatial relationships provide the basis for understanding the structure of social groups; the results of proximity analysis from this study are presented in the previous portion of the thesis (Chapter 3). In order to expand upon the details of the social relationships, it is also necessary to examine the specific behavioural interactions between group members (Hinde 1983; McFarland 1987). Studies with other species (e.g. yellow-bellied marmot: Armitage 1977; meadow vole: Ferkin 1988; tamarin: Goldizen 1989) indicate that social interactions differ at various levels and inter-connect with one another to form the complexities of an established group structure. Therefore, Chapter 4 is organised to separate different social "dimensions", although some overlap is necessary to interweave the connected elements; the subdivision of parts is similar to that of Chapter 3.

This chapter discusses all the behavioural data concerning specific social interactions among the colony cats. Using the skeleton based upon the proximity analysis in the previous chapter, the behavioural results are coalesced to present a more complete picture of the social structure of the study population than is provided by spatial relationships alone. It was necessary to establish the inner workings of the population before examining maternal behaviour more closely, with a view to using reproductive aspects to explain potential pressures acting on cat groups. The following questions shape the chapter: "what are the general behavioural trends for the two study groups of cats (Section 4.2)?"; "what are the differences based on age and sex classes (Section 4.2)?"; "do specific pairs of cats show any differences from other dyadic combinations and from one another regarding initiation and receiving of interactions (Section 4.3)?"; "are there individual differences between the cats, and how do these affect the group (Section 4.4)?"; "what are the seasonal changes in activities (Section 4.5)?"; and, "is there any evidence of group stability in terms of social behaviour and how is it manifested?"

The first consideration was the data itself; the visible availability of each Focal individual is presented (Section 4.1.2.1), along with some calculation of frequency and duration of various behaviour measures (Section 4.1.2.2). The drawback to One-Zero sampling is the absence of information about the temporal patterning of behaviour; using the modified method explained in Section 4.1.2.2, it was possible to overcome this problem to some extent.

Chapter 4 is divided into six major parts. The initial three sections deal with the following different levels of group organisation: the Colony, the Dyad and the Individual. The first, Section 4.2, presents general trends pertaining to the groups, as well

as comparing measures for both the sex and age classes and looking for differences based on these variables. The second section, The Dyad (Section 4.3), breaks down the group behaviour into its component parts, consisting of pairs of individual cats; sex and age classes are again used to examine differences in the initiators and recipients of most social interactions. The third part (Section 4.4) addresses the question of individual differences in behaviour as one of the aspects affecting the social organisation of groups and looks at rates of activity for each group member.

The remaining three parts investigate different aspects of social behaviour. Section 4.5 repeats the techniques used in the previous chapter to look for seasonal changes in social relationships; different activities are examined to ascertain which behaviour patterns might support group stability and act as predictors of other social exchanges (such as reproductive "alliances"). The fifth part (Section 4.6) takes a slightly different set of data and treats it as with the earlier sections to find corroboration for proposed trends; the main body deals with behaviour from 1987, prior to the start of Focal observations, while additional support for Focal aspects comes from Continuous supplemental data. The last section, Scent-Marking (Section 4.7), addresses the literature behind this topic before discussing the results from the present study. Scent-Marking was not presented in earlier sections because of the slightly different nature of the exchange, in which a second animal was not always identifiable (unlike the other social interactions discussed here).

4.1.2. METHODS

Most of the methodological details were fully described in Sections 2.2.2 and 2.4.3 of Chapter 2, but these are supplemented by the following sections, discussing the details of the visible "availability" of Focal individuals, and the estimation of frequency and duration using a modification of the standard method of One-Zero time sampling.

4.1.2.1. *Availability*

Focal Adults in this study were visible for a total of 57175 30-second observation intervals, or just over 476 hours; Focal Juveniles were observed, and in sight, for 17048 intervals, or 142 hours. This gave a total of about 619 hours of observation in which the Focal subject was in sight and therefore available for data recording (an additional 42 hours of the total observation time was spent with the Focal subject out-of-sight). There were some differences between the two groups in terms of the time that individual cats were visible during Focal watches. For Side A, Adults were watched for a mean of 4703.2 periods (39.2 hours) each, with 94.8% of the periods spent in visible view of the observer (or 5.2% of the total intervals out-of-sight). Side A Juveniles were

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observed for a mean of 2516.0 periods (21.0 hours) each; 93.8% of all periods were in sight (or 6.2% out-of-sight). The total for all Side A Focal individuals was a mean of 3828.3 intervals (31.9 hours) each, with 5.5% of the total spent out-of-sight.

On Side B, Adults were focally watched for an average of 4627.6 intervals (38.6 hours) each; 94.0% of the total intervals were visible (6.0% out-of-sight). Juveniles on Side B were watched the least, on average, with only 1722.4 intervals (14.4 hours) each. They were also the least visible group, only in sight 88.3% of the time (and out-of-sight for 11.7% of the Focal watch time). Overall, Side B individuals were focally observed for an average of 3417.1 intervals (28.5 hours), with 7.2% of those periods out-of-sight. In total, cats on Side A were focally watched for 319.0 hours and those on Side B for 341.7 hours. The summarised totals for Adults and Juveniles are shown in Figures 4.1.a and b.

4.1.2.2. *Frequency and Duration*

In order to investigate the intricate webs of interaction and social relationship in the cat groups, overall behaviour categories were chosen. These included several general descriptions, such as "contact", "agonistic" and "mating behaviour". Within each grouping, discrete behaviour patterns were defined and became the units upon which the Focal-animal observations were based.

State and event behaviour modes were both used (Altmann 1974; Bekoff 1979). The Focal method was primarily One-Zero (1/0) sampling (Martin & Bateson 1986), modified to enable the observer to estimate frequency and duration more accurately (than classical 1/0 methods allow). The basic design was a 34-minute checksheet (see Appendix A), divided into 30-second periods (demarcated by rows). A timing-device gave a short, loud bleep through an earphone; with each tone, a new row was started. The name of interactants and the direction of interaction were noted for each behaviour. If the action was repeated more than once in a 30-second interval, this was also recorded.

All summaries of Focal behaviour have been derived from the standard 1/0 method, and are, in fact, measures of the number of 30-second intervals in which a particular behaviour was observed. To supplement this, and to justify the use of 30 seconds as a time limit, actual frequencies have been found for each event behaviour. For those behaviour patterns which are more accurately described as "states", an approximate measure of duration has been calculated. The margin of error in duration counts derives from the fact that they have been found from 1/0 measures (and not actual start-stop times); each count is +/- 58 seconds. A break of 30 seconds or more was used to define bouts.

Figure 4.1.a

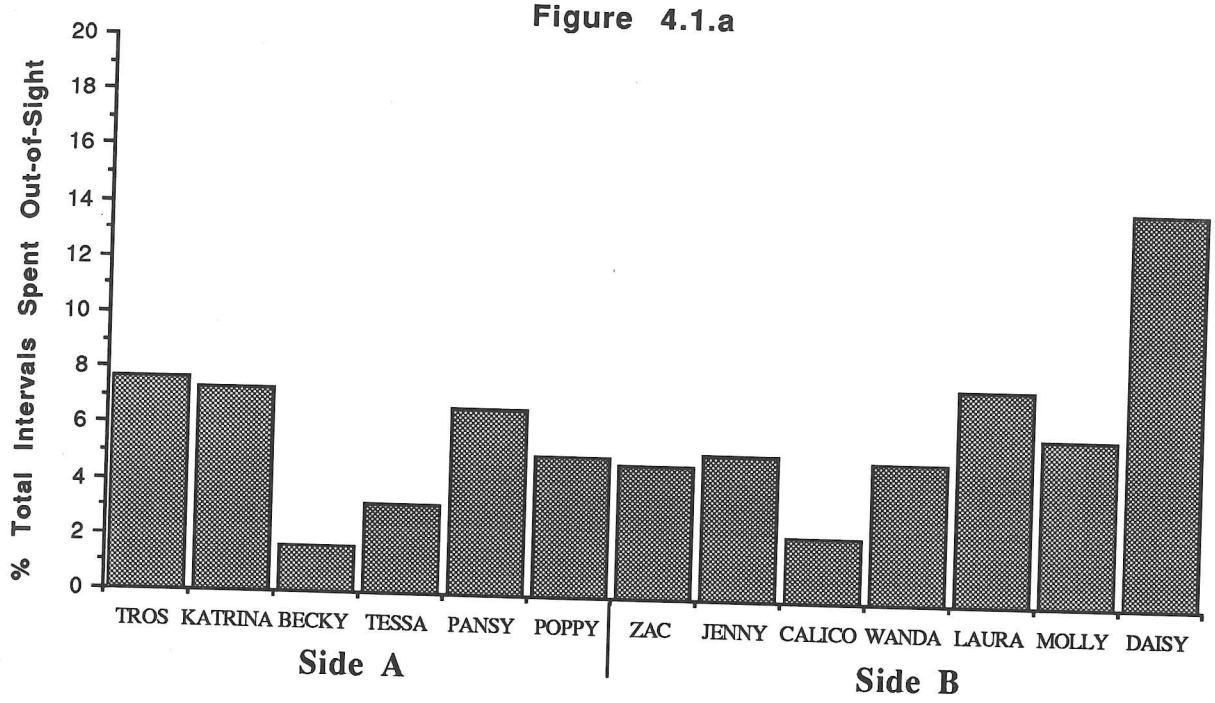


Figure 4.1.b

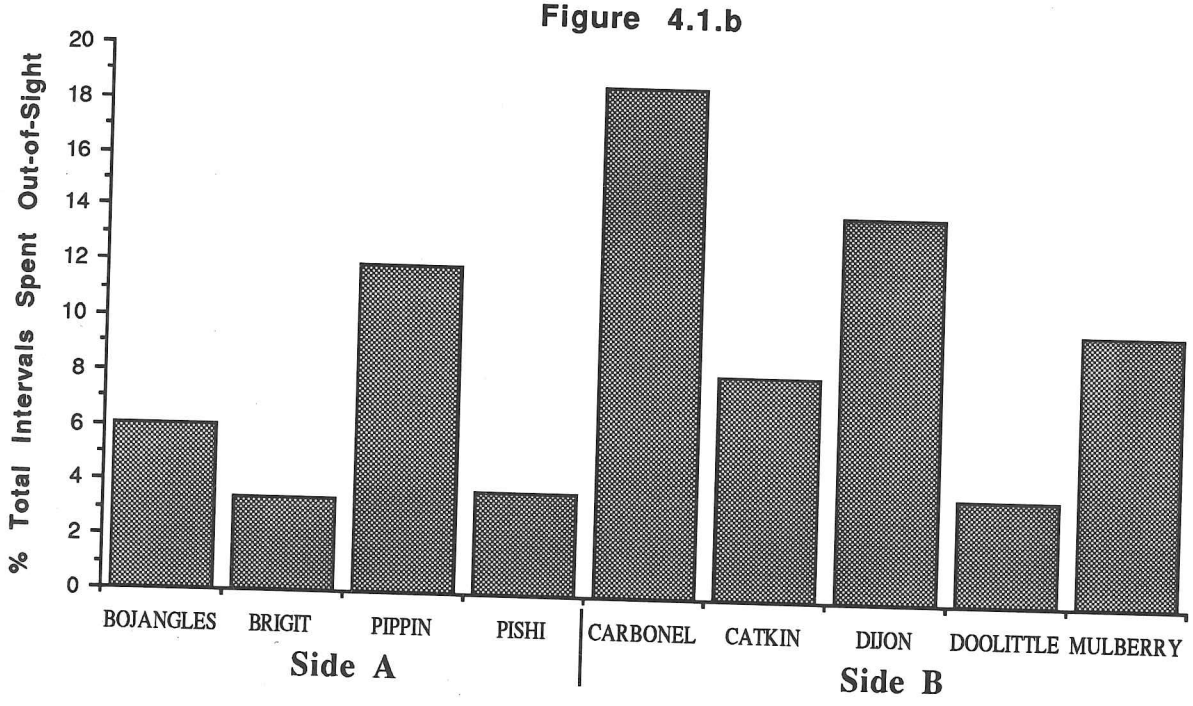


Figure 4.1: The proportion of Focal observation time spent out-of-sight by each individual. The members of each of the two groups are indicated. (a) Adults; (b) Juveniles.

4.1.2.2.i. *Frequency*

All Focal observations were considered. The total number of intervals in which a specific behaviour occurred once or more than once (up to six times) were found. Descriptive statistics were calculated using Statview 512+ on the Macintosh computer. The mean refers to "the mean number of times a behaviour occurred per 30 second interval". The following behaviour patterns were considered as events: Follow, Approach, Evade, Cheek/Head Rub, Body Rub, Close Sniff, Paw, Swipe, Bite, Fight, Mount, Scratch, Vocalise (Hiss/Growl, Meow, Yowl), and Marking (by rubbing, as opposed to spraying). Other possible event categories occurred too rarely to calculate frequency (Bite, Ear Flattening, Piloerection, and Tail Lashing).

Most categories proved to occur only once (on average) in a 30-second period (Figures 4.2.a & b). Notable exceptions were Meow (mean= 1.99), Mark (by rubs; mean= 1.54) and, to some extent, Swipe (mean= 1.35) and Yowl (mean= 1.34). It would appear that most behaviour patterns sampled in this study occurred less than once every 30 seconds (giving a mean rate around 1.0, calculated by dividing the actual frequency by the number of intervals in which the activity was recorded). Therefore, it seems reasonable to use the number of 30-second intervals as a fairly accurate estimator for most behaviour categories, with additional consideration to those that are repeated once initiated.

One feature was that the behaviour patterns that strayed most from a mean of one per interval were those that tended to be performed less often, and involved no direct contact with the recipient; Swiping was the single exception, and it often was as much a threat of injury as involving any actual contact. Some patterns were prone to occur as bouts, and once performed, they were commonly repeated; Meow and Mark were especially clear examples of this.

4.1.2.2.ii. *Duration*

All Focal observations were considered. Series of consecutive occurrences between a particular dyad were used as counts. Any break in the continuity of 30 seconds or more (as represented by a non-occurrence in an intervening interval) defined the end of the "bout". Descriptive statistics were produced using Statview 512+, as with the frequencies. In this case, mean refers to "the mean number of consecutive 30-second periods in which the behaviour was observed". It is likely that they are underestimates of the actual durations (but within a minute or so). The following were primarily considered behavioural "states", and therefore durations were calculated: Rest/Sleep in Contact, Nurse, and Groom. Also, Follow, Mount and Play were perhaps performed for longer than 30

Figure 4.2.a

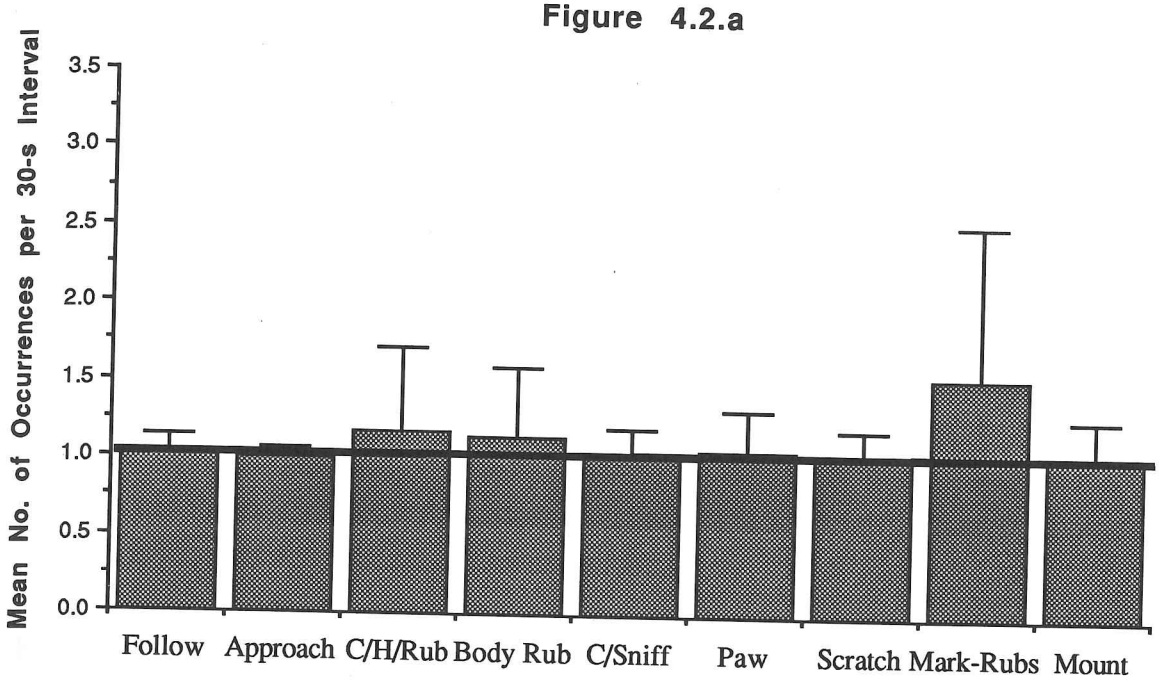


Figure 4.2.b

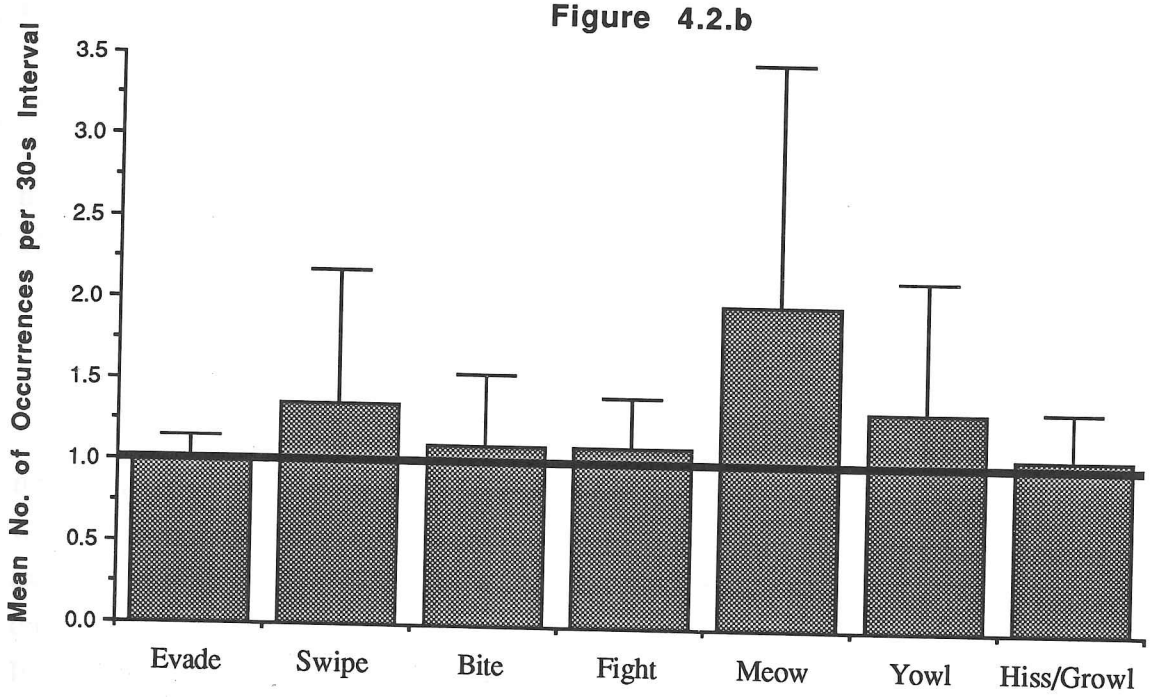


Figure 4.2: The mean frequency of Focal activities, expressed as the number of occurrences per 30-second observation interval. The level "1.0" indicates the condition in which a 30-second interval approaches the accuracy of Continuous recording. **(a)** General and Affiliative Behaviour; **(b)** Agonistic and Vocalisation Behaviour.

seconds. Certain other behaviour categories were too rare to consider duration aspects; these included Ear Flattening, Piloerection, and Tail Lashing.

Most behaviour patterns were of relatively short duration (Table 4.1). Nurse and Rest/Sleep in Contact were the two states which tended to occur over long periods (Nurse: mean= 14.0 intervals or 7 minutes; Rest/Sleep: mean= 25.6 intervals or nearly 13 minutes). Both of these categories are complicated by additional features: Rest/Sleep in Contact measures were derived only from the Focal individuals, and therefore subject to a maximum of 68 continuous intervals; if two animals, joined together in this behaviour, were observed consecutively, the true duration might be as high as 136 intervals (or more with groups of three or greater). Therefore, the duration considered here must be taken, not as the true length of Rest/Sleep in Contact, but as the mean amount of time per 34-minute watch which might show the behaviour.

Nursing behaviour was similarly complicated. The duration of Nursing for each Kitten was scored separately and can therefore overlap. Thus, the value does not necessarily reflect the total time (per watch) spent suckling by the Female; in fact, the measure describes the time spent suckling by a Kitten in the average Focal watch. Sometimes there was only one score for multiple Kittens where a litter of young Kittens was involved. It was also possible to find the mean when a Female was suckling Kittens in general, without naming individuals (and without accounting for individual bouts); in that case, the mean Nurse duration increased slightly from a mean of 14.0 to a mean of 16.9 intervals (8.5 minutes).

4.1.2.3. *Other Aspects Regarding Behaviour Data*

The majority of recorded Focal behaviour patterns proved to be rare, involving only a small portion of the total observation time. The more common activities were numerous enough to allow weekly, monthly, seasonal and yearly summation, as well as consideration of specific dyadic exchange; on the other hand, "rare" behaviour could only be considered on a more lumped scale, by initiator and recipient, dyad, and group. In-depth examination was performed with the following behaviour: Follow, Approach, Evade, Cheek/Head Rub, Body Rub, Close Sniff, Groom, Swipe, and Rest/Sleep in Contact. All other Focal interactions were analysed more generally, and lacked the sample size for the specific tests. Capitalised words denote variable factors in this chapter, including behaviour categories, as well as age and sex classes.

Table 4.1: Duration Measures for Some Focal Behaviour Patterns, as Derived from One/Zero Watches (expressed as the number of 30-second periods)

Behaviour	Mean	sd	n	Range
Follow	1.367	.69	781	1-7 periods
Rest/Sleep in Contact	25.570	22.87	707	1-68 periods
Object Play	2.350	2.41	37	1-10 periods
Social Play	2.210	2.19	90	1-15 periods
All Play	2.250	2.24	127	1-15 periods
Mount	5.116	6.11	43	1-37 periods
Nurse	14.015	12.87	131	1-68 periods
Self Groom	3.517	4.89	1549	1-55 periods
AlloGroom	2.587	3.12	433	1-31 periods

4.2. THE COLONY

4.2.1. FEMALE RELATIONSHIPS

All Adults were described at the "Colony" level for the nine most common actions, and they were compared for Female-Female, Female-Male and Male-Male sums (Figure 4.3.a), as well as for the average amount of each behaviour for Females versus Males (Figure 4.3.b). The hourly rates are summarised in Table 4.2.a, based on the number of intervals a behaviour was seen per hour watched. These can then be divided by the possible number of particular types of dyads to give an average rate; Males Follow and Close Sniff Females at the highest rate, Females Evade and Swipe Males the most, and all other actions are greatest for Female-Female combinations (Approach, Rubbing, Grooming and Resting in Contact). The differences between the sexes over all interaction rates were not significant (χ_r^2= 3.059, p= .217, df= 2, n= 9), but Female-Female actions ranked before Female-Male and then Male-Female. Each combination of initiator and recipient (e.g. Females to Females) was treated as a "block" for this test, with rates of specific behaviour patterns as the matched variable. As with the Friedman's tests performed in Chapter 3, the statistic refers to the entire set of blocks and not to individual comparisons. The three Male and Female combinations were generally correlated together, indicating a roughly consistent level of interaction based on specific behaviour and less on particular interactants (Table 4.2.b).

When the two groups were compared, no difference was found using a Wilcoxon matched-pairs test (Z= -1.304, p= .192), which matched the two groups across the group rate (found over all Adults in a group) for each behaviour pattern. This lack of differences held true when each behaviour pattern was tested using a Mann-Whitney U-test; the two sides were compared for each of the nine behaviour rates, using the number of initiations per interval of observation for each Adult cat (n= 6 in Group A and 7 in Group B). None of the differences in the rates of behaviour between the two groups were significant (Follow: U= 18, Z= .429, p= .6682; Approach: U= 18, Z= -.429, p= .6682; Evade: U= 19, Z= -.286, p= .7751; Cheek/Head Rub: U= 14.5, Z= -.930, p= .3524; Body Rub: U= 16, Z= -.718, p= .4726; Close Sniff: U= 18, Z= -.429, p= .6682; Swipe: U= 13, Z= -1.143, p= .2531; Groom: U= 13, Z= -1.176, p= .2398; Rest/Sleep in Contact: U= 9, Z= -.1.714, p= .0865). In fact, the two sides were linearly related across the rates for all behaviour patterns (r_s= .933, Z= 2.64, p<0.01), such that behaviour patterns were performed at similar relative levels in both groups. Mean group rates are given in Figure 4.3.c. For all following analyses, the two groups were pooled for general Male and Female analyses, but were treated separately for discussions of specific dyads and individuals.

Figure 4.3.a

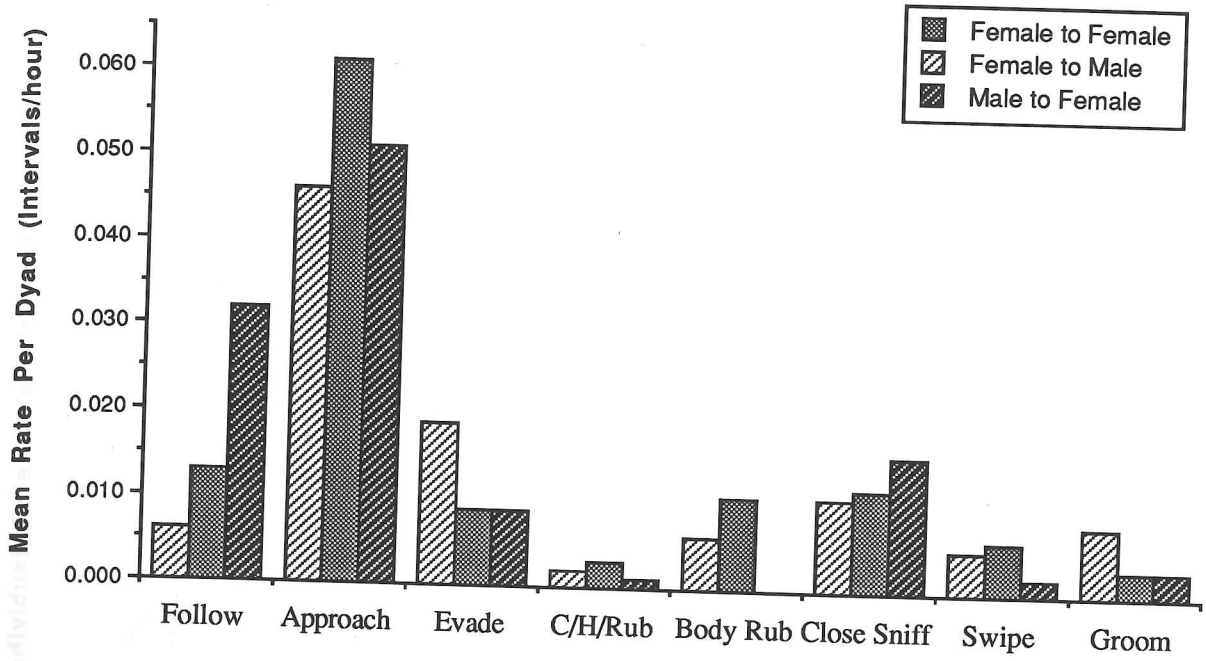


Figure 4.3.a: The mean rate of common behavioural interactions between Females and Males. Averages were found using all Adult-Adult dyads in both cat groups, and are expressed as the number of observation intervals per hour in which each activity was seen.

Figure 4.3.b

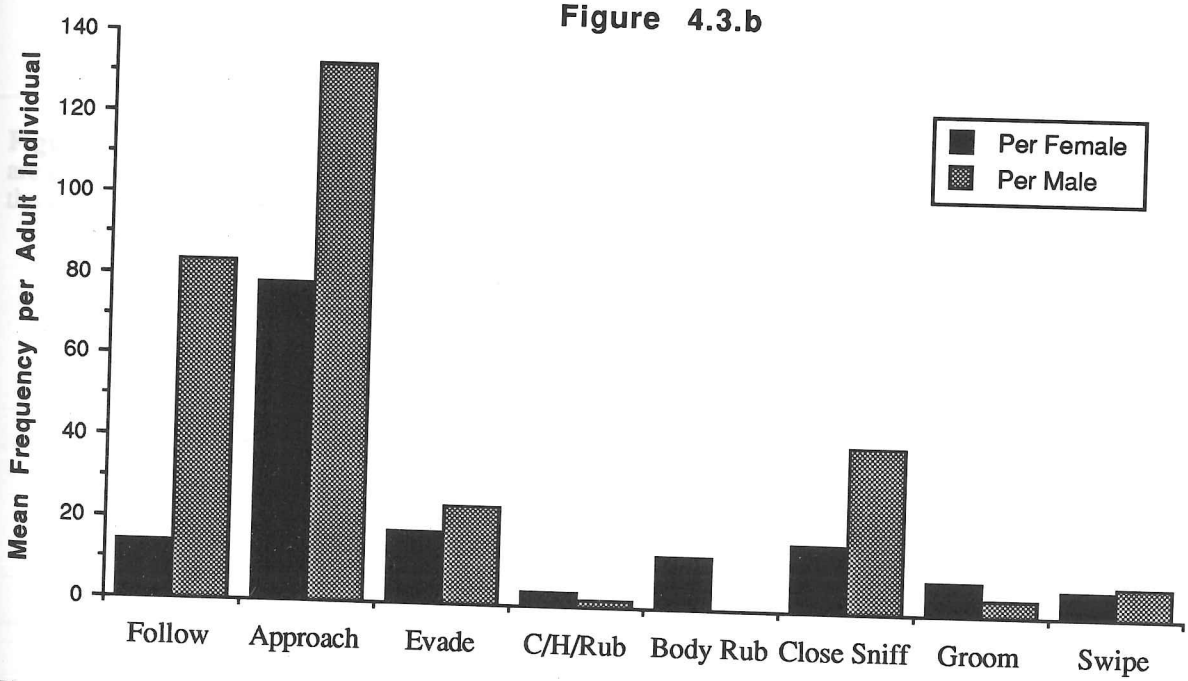


Figure 4.3.b: The mean frequency of common behavioural interactions initiated by Adult Females and Males. Averages were found using the sum of all initiations by each sex class and the number of possible animals; Females: n=11, Males: n=2.

Figure 4.3.c

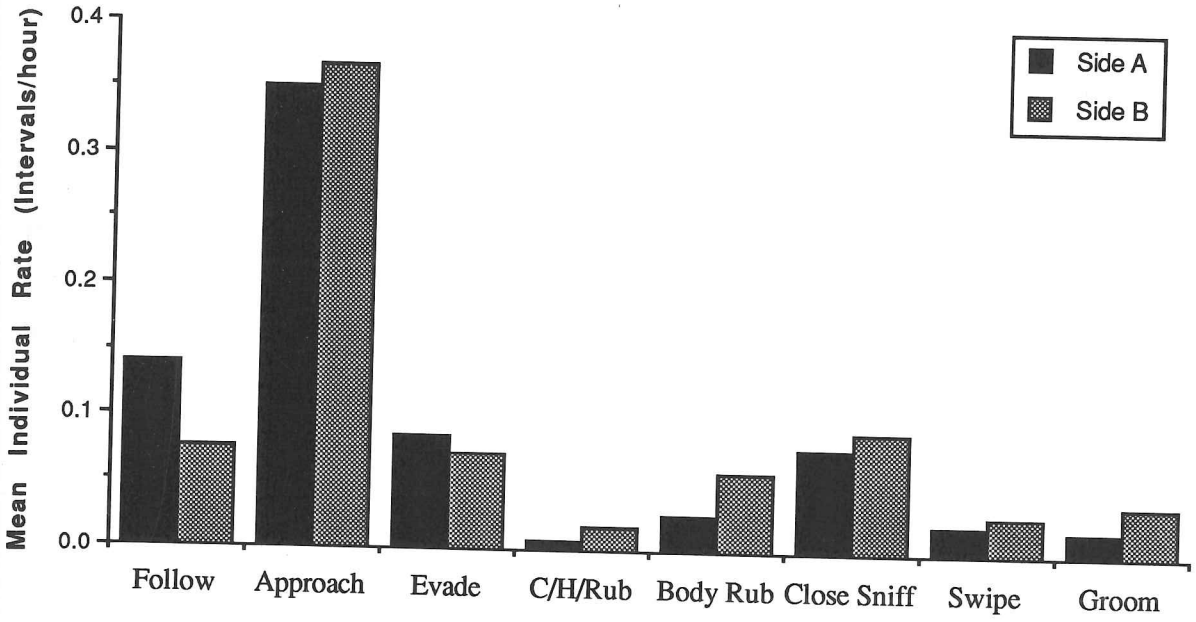


Figure 4.3.c: The mean rates of common behavioural interactions for the two groups of cats. Rates are expressed as the mean number of intervals per hour (over all Adult members of each group) in which the activity was observed. Group A: n=6, Group B: n=7.

Table 4.2.a: Hourly Rates of Common Focal Behaviour Between Adults

Behaviour	**Female-Female** (n=25)	**Female-Male** (n=11)	**Male-Female** (n=11)
Follow	.320	.061	.348 †
Approach	1.532 †	.504	.556
Evade	.235 †	.204	.103
Cheek/ Head Rub	.069 †	.027	.008
Body Rub	.283 †	.063	0
Close Sniff	.307 †	.124	.172
Rest in Contact	10.737 †	1.786	1.224
Groom	.158 †	.050	.017
Swipe	.069 †	.086	.031

(† = highest rate)

Table 4.2.b: Spearman Correlations Between Sex Classes for Common Actions. Tests were performed comparing the ranked rates of interaction over 9 behaviour patterns. A significant result means that interaction rates are ranked with a linear relationship between the two groups, e.g. Female to Male interaction rates correlate with the rates from Males to Females.

Group 1	**Group 2**	**n**	r_s	**Z**	**p**	
Female-Male	Female-Female	9	.689	1.949	.051	
Female-Male	Male-Female	9	.787	2.225	<0.05	*
Female-Female	Male-Female	9	.803	2.272	<0.05	*

The remaining behavioural descriptions refer to less common activities, or "rare" behaviour. Pawing, or reaching to touch another individual with a forepaw in a non-agonistic context, was mainly performed by Adult Females to other cats, and by Kittens. Some Pawing was seen from Juvenile and Adult Males, and Females were always the recipients of such gestures. Adults delivered 52% of all Paws, Juveniles gave 22%, and Kittens contributed 26%, mainly toward Adult Females. A total of 98 Paws were recorded over the Focal observation period. Female-Female encounters accounted for 38% of all Adult-Adult Paws, and were supplemented by interactions between Juvenile and Adult Females (11%). It is unlikely that this type of action has any functional purpose other than initiating and maintaining contact between two non-aggressive cats; Pawing was often observed between two cats resting together, including mothers with their Kittens, and may not have been more than a stretching movement which was characteristic of a relaxed relationship.

Ear Flattening was considered to be a gesture of threat or defence, and involved a marked change in ear posture, rather than just the slight perking and swivelling seen in alert individuals. Once flattened, ears were often held in this position for some minutes, so that the numbers of intervals undoubtedly overestimate actual frequencies. The vast majority of incidences involved only the Focal individual, with no obvious interactant (89-92% of all cases). Cats on Side B Ear Flattened about twice as much as Side A cats, and the increase was particularly large for Juveniles (93% of the total intervals in which the behaviour was seen). Over half the observations were from Females, both Adults (55%) and Juveniles (4%). Adults contributed 90% of all observations. The behaviour was seen in both conflict and non-conflict situations, sometimes involving mating attempts and interactions between older Kittens and Females.

Tail Lashing was similar to Ear Flattening, both in its duration and the context in which it was observed. Again, Females exhibited over half the observed examples, with Adult Females contributing 54% and Juveniles 8%. Adults performed 80% of all Tail Lash intervals, predominantly those cats from Side B. The majority of all incidences were not visibly directed at any specific other, ranging from 73% in Group A to 81% in Group B, 78% of Female numbers and 81% of Male counts.

Piloerection was another "agonistic" behaviour which was seen very rarely. A total of 26 periods were recorded for this action, all performed by Females; Adult Females to other Adult Females accounted for 31%, and those to no recipient made up 50%. Adult Males received 8%, Juvenile Females 4%, and Kittens 4% (the last 4% was between two Juvenile Females). Only some individuals were seen to erect their fur (Piloerection), and this is discussed further in Section 4.4.1.

Two types of Play were recorded, to get a rough idea of these particular activities in outside cats. The first was Object Play, involving a cat with an "inanimate"

object; On Side A, only Females were observed engaged in this action (n=26), and 23% involved a prey animal (usually dead and/or inedible). On Side B, there was generally more of this behaviour, including equal numbers from Males and Females (n=74), and including 11% with prey animals. Side B Adults (mainly Females) performed 38%, while Juveniles contributed the remainder of the observations.

Social Play was the second form, and it was observed to take up more intervals than Object Play (n=217). Adult-Adult interactions came to only 3% of the total (although they initiated 10%, including those with Juveniles and Kittens), and were a minor part of Adult behaviour and Play behaviour. The vast sum of these encounters involved Kittens, and are therefore discussed further in Section 4.2.4.

Cats were seen to Scratch objects including trees and other upright structures. The function and details of tree-scratching are discussed under Scent-Marking (Section 4.7); overall, Females performed more Scratching than Males (83%), and the average Female contributed 19 Scratches to the 8.6 of the average Male (Adult Female mean=21, Adult Male mean=11). Females on Sides A and B evinced similar amounts of Scratching, while Side A Males Scratched somewhat more than Side B Males (A mean=14, B mean=6).

4.2.2. MALE RELATIONSHIPS

Of the nine major behaviour patterns, most of the general colony-level results are presented in the preceding section, along with the Female measures. Figure 4.4.a demonstrates the differences in total interval frequency for each behaviour, based upon initiator (Male or Female) and recipient (Male or Female)

Activities concerned with mating were predominantly confined to Female-Male interactions, although Males were seen Mounting inappropriate individuals, including young Kittens of both sexes and Male peers. A total of 202 intervals were spent engaged in Mounting, including 48 separate Mount attempts. Trossachs performed 71.4% of all Mounts in his group, while Zac was seen to contribute 55.6% of the B group Mounts. Adult Females were the primary recipients (67%), with Juvenile Females (18%), Female Kittens and Juvenile Males receiving the other attempts. Copulation and the Female Response were less frequent; 47% of Mounts led to intromission in Side A, whereas 33% of Side B Mounts involved intromission. Successful Mounts, with intromission, were seen only with Females, never when a Male or Kitten was the subject of attention. All Focal Males were seen to Mount at least once, although frequency varied among individuals.

Lordosis and Rolling were not recorded as Focal behaviour, but were noted for all occurrences in the course of data collection. Lordosis was very rarely seen (n=9),

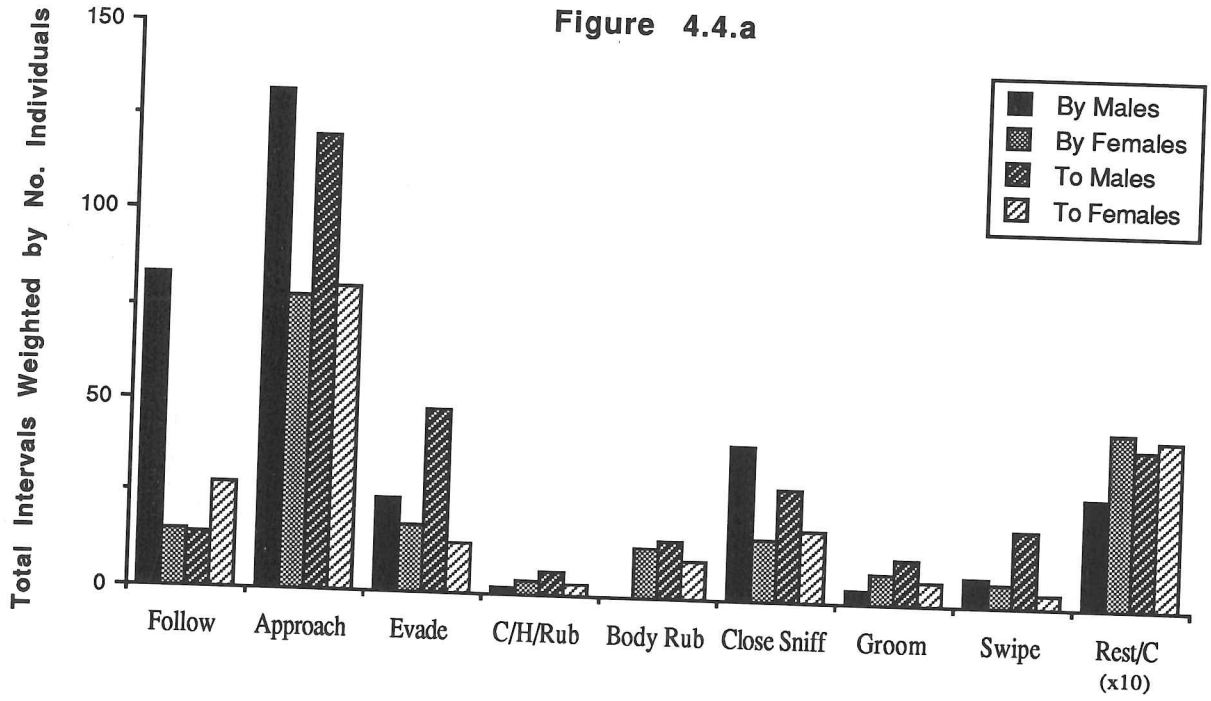


Figure 4.4.a: The total interval frequency for the most common behavioural activities. "By Males" and "By Females" indicate the frequencies initiated by each sex class; "To Males" and "To Females" denote the frequencies received by each sex class. Only Adults are included here. Measures are weighted by the number of Females (n=11) and Males (n=2). Note that Rest in Contact (Rest/C) is shown at one-tenth its level, in order to display all the activities on one figure.

Figure 4.4.b

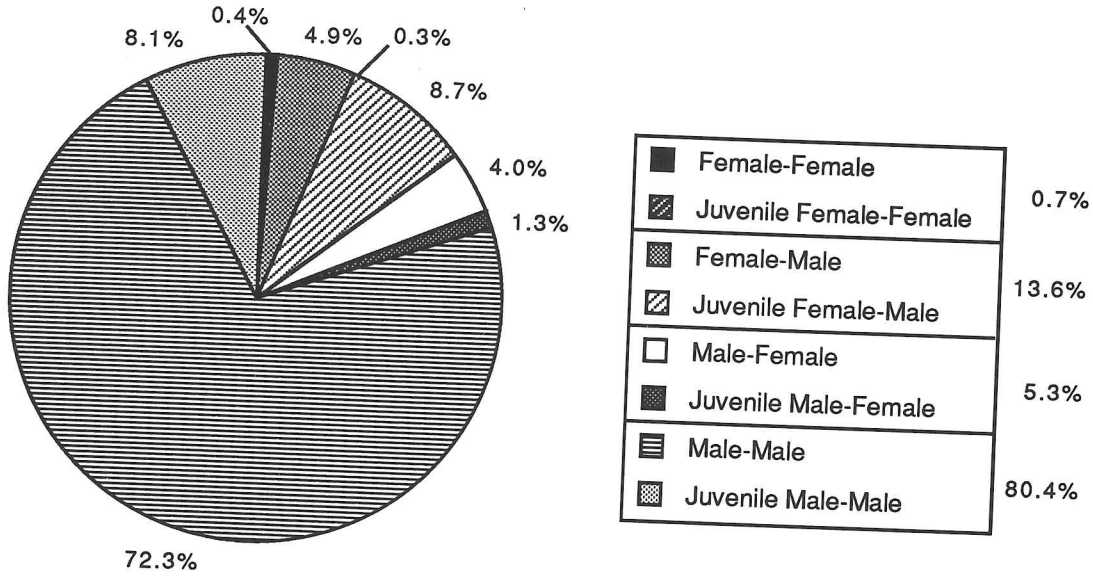


Figure 4.4.b: The proportion of Rolling behaviour initiated and received by each age and sex class. Totals are divided into initiators and recipients in the legend, such that the first block corresponds to Female-Adult Female Rolls, the second block to Female-Adult Male Rolls, the third block to Male-Adult Female Rolls, and the fourth block to Male-Adult Male Rolls. All values are weighted by the number of dyads, and therefore correspond to "per capita" rates.

and was performed twice as often by Side A Females. The majority of observed Mount attempts were not preceded by lordosis in the Female. Rolling has been described as an additional form of Female solicitation for mating; a total of 174 Rolls were recorded, and only 40% of these were performed by Females (57% of Female Rolls were to Males). The remainder were contributed by Males; 30% of all Rolls were Male-Male (half by Juveniles to Adults; Figure 4.4.b shows the rates per dyad type, or "per capita"). There was some indication that Rolling was not just involved in Female-Male encounters, but may also be some form of submission or appeasement behaviour, as seen in other carnivores.

Biting was rare, and a total of 21 Bite intervals were observed; 36% of these were seen in the context of Mounting, wherein the Male grasps the Female's nape between his teeth. Just over half the Bites were delivered by Males to Females (52%), 29% were from Females to Males, and 14% were Males to other Males. Juveniles contributed only 5% of the total number of Bites, and Adult Males were the main initiators. Aside from mating, Biting was seen in agonistic situations, although contact was almost never achieved, and occasionally in the course of tending Kittens, as if to deter the Kitten from suckling. Fighting was also uncommon, and most of the observations were taken from non-Focal watches, and will be discussed in Section 4.6; of the 8 fights seen focally, 5 involved two Males (63%), the others were Female-Male and Female-Female. Rarely did interactions escalate to full Fighting, and those that did were usually in the context of Kitten-guarding or Male-Male competition. The enclosures were sufficiently small that the presence of several mature Males (in 1989) sparked numerous disputes, never over any obvious resource (food, water or females) but perhaps due to spatial constraints.

4.2.3. JUVENILE RELATIONSHIPS

The nine most common behaviour patterns were examined in several ways; the first was an analysis of individual Juveniles and how they apportioned their attentions, which is discussed in Section 4.4.3. The second consideration was the overall pattern of each activity and the third was the relationship between activities; these latter two subjects are covered here.

Of the observed categories, all but Resting and Grooming were predominantly directed to Adults (Figure 4.5.a); the remaining two activities involved Kitten recipients. Therefore, Juvenile cats preferentially Followed, Approached, Evaded, Rubbed (Cheek/Head and Body), Close Sniffed and Swiped Adults; with most of these actions, the second most common recipients were other Juveniles, with Kittens trailing at the rear. Each behaviour showed individual differences in the levels to each age category, and these are discussed in Section 4.4.3, but the overall trend is clear. The two groups also displayed differences in the amounts and rates of each major behaviour pattern (Figure

Figure 4.5.a

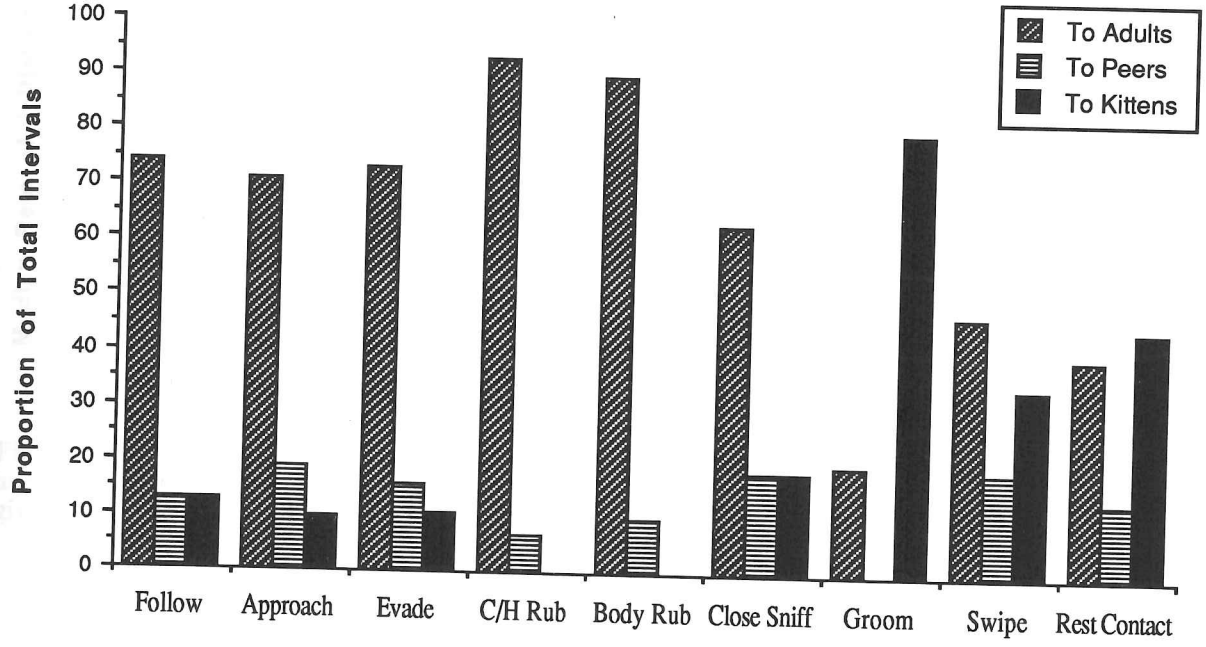


Figure 4.5.a: The distribution of recipients for Focal behaviour patterns initiated by Juveniles. Values given are the proportion of the total number of intervals initiated by Juveniles for each activity. Both Group A and Group B individuals are pooled here.

Figure 4.5.b

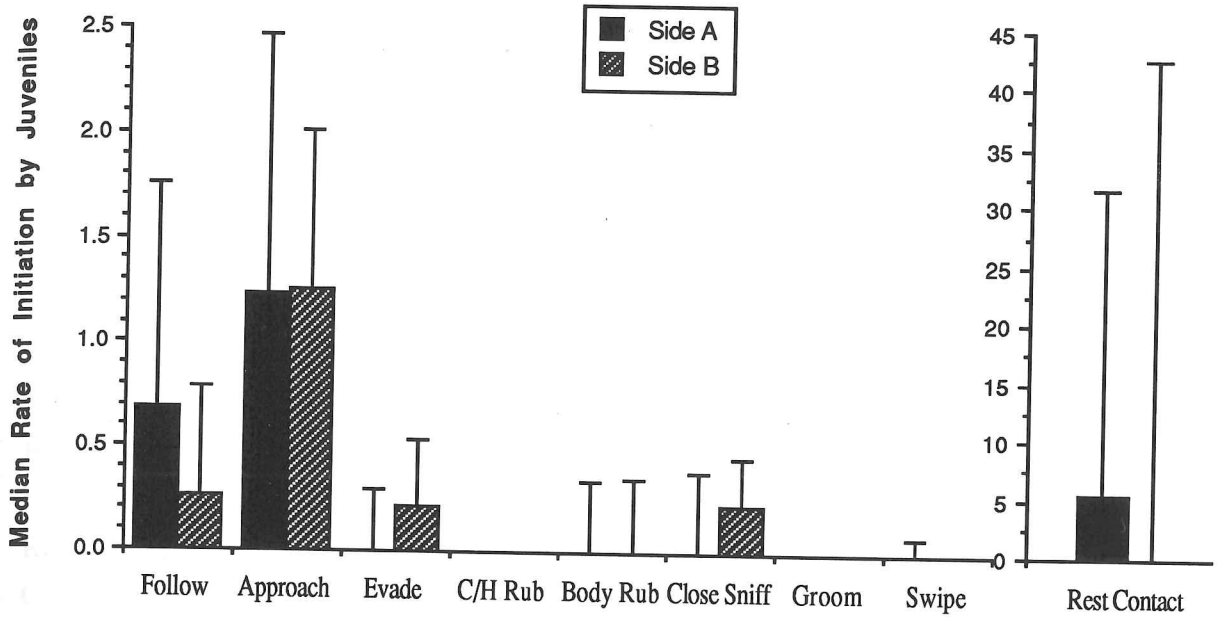


Figure 4.5.b: Group Differences in the rate of behavioural initiations by Juveniles. The rate is the number of intervals per hour summed over all group Juveniles. Medians and interquartile ranges are given. Note the change of scale for Rest in Contact.

Figure 4.5.c

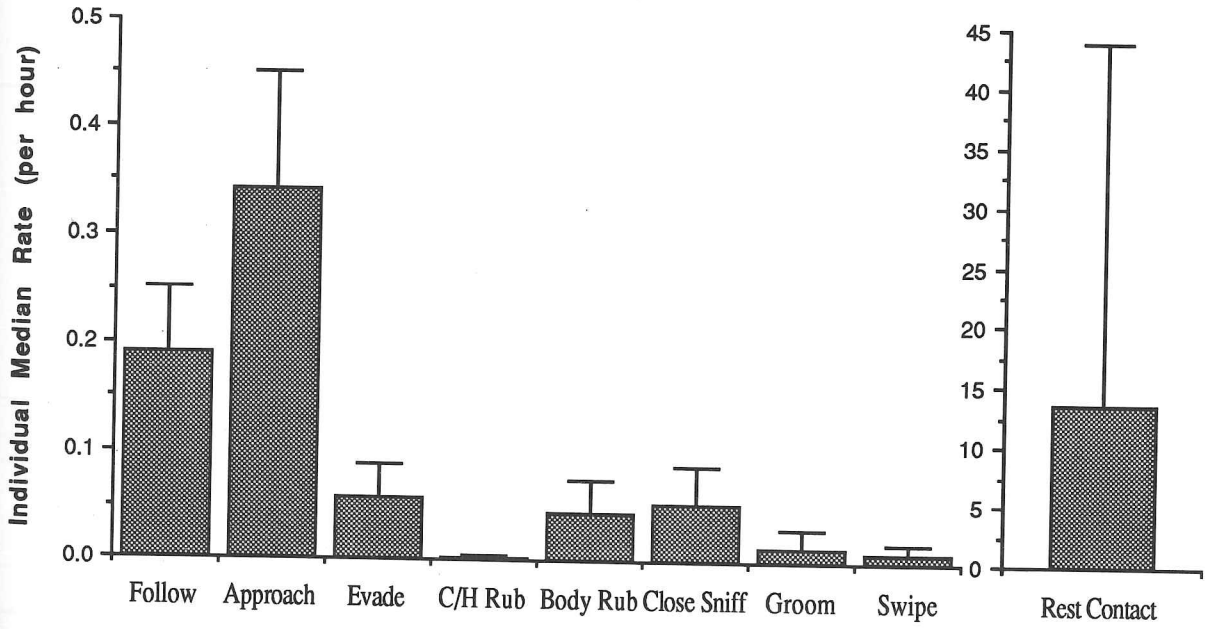


Figure 4.5.c: The rate of behavioural initiations over all Juvenile individuals. The rate is the number of intervals per hour. Medians and interquartile ranges are given. Note the change of scale for Rest in Contact.

Table 4.3 a: Spearman Correlation of Rates of Behaviour Between Juvenile Groups. A significant result would indicate a linear relationship between the ranks of the behaviour rates for Juveniles in Group A versus Group B. The lack of correlations suggests that Juveniles do not interact at a rate determined by their age, but show individual variation, as with Adults.

Behaviour	**n**	r_s	**Z**	**p**
Follow	49	.088	.610	.542
Approach	49	.271	1.878	.060
Evade	49	.192	1.327	.184
Cheek/Head Rub	49	-.140	- .972	.331
Body Rub	49	.251	1.740	.082
Close Sniff	49	.029	.204	.838
Rest in Contact	40	-.223	-1.390	.165
Groom	49	.094	.652	.514
Swipe	49	.053	.364	.716

Table 4.3.b: Correlations Between the Weekly Rates of Behaviour in Two Groups. A significant result means that the two behaviour patterns being compared have linearly related (ranked) rates of initiation over the weeks of observation. Note again that, due to the large number of variables tested together, significance levels should be taken as indicative and not absolute. Two illustrative transition matrices are provided in the following Figures (4.5.d & e), for Approach (as a common behaviour) and Evade (as a possible clue to social structure), including Adult dyads only.

	Side A (n=51)				Side B (n=52)			
Behaviour	r_s	Z	p		r_s	Z	p	
Foll-Appr	.636	4.497	<0.001	***	.372	2.658	<0.01	**
Foll-Evade	.053	.375	.708		.275	1.959	.050	
Foll-C/H/R	.333	2.352	<0.05	*	.105	.749	.454	
Foll-B/Rub	.578	4.088	<0.001	***	.329	2.348	<0.05	*
Foll-C/Snf	.481	3.403	<0.001	***	.065	.464	.643	
Foll-Rt/Sl/C	-.086	- .565	.572		-.160	-1.051	.293	
Foll-Groom	.068	.483	.629		-.257	-1.837	.066	
Foll-Swipe	-.026	- .181	.856		.231	1.650	.099	
Appr-Evade	.322	2.280	<0.05	*	.221	1.580	.114	
Appr-C/H/R	.259	1.830	.067		.193	1.377	.169	
Appr-B/Rub	.510	3.605	<0.001	***	.297	2.118	<0.05	*
Appr-C/Snf	.656	4.638	<0.001	***	.612	4.373	<0.001	***
Appr-Rt/Sl/C	-.195	-1.280	.201		.190	1.246	.213	
Appr-Groom	.039	.278	.781		-.077	- .552	.581	
Appr-Swipe	.019	.137	.891		.257	1.834	.067	
Evade-C/H/R	-.171	-1.207	.228		.233	1.661	.097	
Evade-B/Rub	-.073	- .516	.606		.034	.246	.806	
Evade-C/Snf	.181	1.278	.201		.061	.434	.664	
Evade-Rt/Sl/C	-.215	-1.409	.159		.005	.034	.973	
Evade-Groom	-.040	- .285	.776		-.106	- .755	.450	
Evade-Swipe	-.016	- .113	.910		.186	1.329	.184	
C/H/R-B/Rub	.134	.949	.342		.376	2.687	<0.01	**
C/H/R-C/Snf	.212	1.502	.133		.358	2.556	<0.05	*
C/H/R-Rt/Sl/C	-.067	- .440	.660		.118	.772	.440	
C/H/R-Groom	-.125	- .885	.376		-.091	- .651	.515	
C/H/R-Swipe	-.034	- .241	.810		.154	1.102	.271	
B/Rub-C/Snf	.453	3.202	<0.01	**	.157	1.119	.263	
B/Rub-Rt/Sl/C	-.145	- .948	.343		-.127	- .835	.404	
B/Rub-Groom	.077	.547	.584		-.169	-1.208	.227	
B/Rub-Swipe	.009	.061	.951		.064	.459	.646	
C/Snf-Rt/Sl/C	-.090	- .588	.557		.274	1.794	.073	
C/Snf-Groom	.029	.205	.838		.300	2.145	<0.05	*
C/Snf-Swipe	.276	1.949	.051		.229	1.637	.102	
Rt/Sl/C-Groom	.237	1.556	.120		.200	1.314	.189	
Rt/Sl/C-Swipe	-.079	- .521	.603		.176	1.156	.248	
Groom-Swipe	.134	.947	.343		.147	1.051	.293	

Figure 4.5.d

Recipient

Initiator: APPROACH	Trossachs	Katrina	Becky	Tessa	Pansy	Poppy
Trossachs		46	18	25	21	29
Katrina	10		1	2	4	11
Becky	9	8		29	3	9
Tessa	12	6	24		4	11
Pansy	37	9	10	23		3
Poppy	20	59	7	8	11	

Recipient

Initiator: APPROACH	Zac	Jenny	Calico	Wanda	Laura	Molly	Daisy
Zac		31	23	17	23	16	16
Jenny	28		19	23	17	35	10
Calico	35	24		18	11	7	3
Wanda	51	34	25		10	14	5
Laura	23	8	6	10		10	5
Molly	12	58	3	4	3		2
Daisy	3	1	1	4	4	2	

Figure 4.5.d: Transition matrices showing the raw data for Approach between Adults. The top matrix is Group A, and the bottom matrix is Group B. The Adult Male of each group is given as the first name in the matrix (e.g. Trossachs and Zac). Individuals along rows are initiators of Approaches, while those along columns are recipients of Approaches (or are "approached").

Figure 4.5.e

Recipient

Initiator: EVADE	Trossachs	Katrina	Becky	Tessa	Pansy	Poppy
Trossachs		3	4	9	5	7
Katrina	23		0	0	0	5
Becky	4	0		1	1	0
Tessa	6	0	0		2	1
Pansy	9	4	1	2		6
Poppy	13	2	2	1	2	

Recipient

Initiator: EVADE	Zac	Jenny	Calico	Wanda	Laura	Molly	Daisy
Zac		1	1	9	8	0	2
Jenny	5		1	5	3	4	1
Calico	6	2		3	0	3	0
Wanda	7	3	2		1	1	3
Laura	10	0	1	0		0	2
Molly	4	2	1	3	1		0
Daisy	10	11	4	2	0	6	

Figure 4.5.e: Transition matrices showing the raw data for Evade between Adults. The top matrix is Group A, and the bottom matrix is Group B. The Adult Male of each group is given as the first name in the matrix (e.g. Trossachs and Zac). Individuals along rows are initiators of Evades (or avoid the named recipients), while those along columns are recipients of Evades (or are "evaded").

4.5.b). Despite the fact that the Juveniles were watched for a similar number of hours each week (Side A median=4.9, Side B median=5.5; r_S= .836, Z= 6.37, p<0.001), the rates of all behaviour patterns were not correlated between the two groups of cats (Table 4.3.a), demonstrating that Juveniles do not interact at a rate determined mainly by their age, but vary among themselves.

Correlations were performed with each group, across all dyads (including those with Juveniles), to look for associations between separate Focal activities. The two groups showed different patterns of association (Table 4.3.b and Figures 4.5.d & e), such that, for Side A, increases in Follow rate were significantly related to increases in the rates of Approach, Cheek/Head Rub, Body Rub and Close Sniff, while Approach was positively correlated with Evade (and Body Rub and Close Sniff), and Body Rub rates increased with Close Sniff rates. Side B Juveniles had slightly different associations, all positive, between Follow, Approach, Body Rub and Evade, as well as Approach and Cheek/Head Rub with Close Sniff and Close Sniff with Groom. As will be examined later, these correlations were probably related to certain forms of behaviour shown in different seasons, such that in the gestation period (often late winter to early spring), Juveniles Followed Females quite a lot, and initiated some Rubbing, which was often rebuffed; also in the colder weather, there was more Resting in Contact. Much of the more affiliative behaviour was displayed during the breeding season, and so correlations were found.

When all Juveniles were included in the correlation of behaviour rates, a few significant overall trends were found; Follow increased with Approach (p<0.05) and Swipe (p<0.01), Approach increased with Close Sniff (p<0.01), and Cheek/Head Rub increased with both Body Rub (p<0.05) and Rest in Contact (p<0.05). Thus, the rate at which an individual Juvenile Followed other cats was related to the rate at which it Approached and Swiped; the rate at which individuals Approached was associated with Close Sniffing rates. And Rubbing rates were correlated to one another and to the initiation of Contact Resting.

When all nine patterns were compared for the initiating rates shown over all Juveniles, a significant difference was found (χ_r^2= 51.521, p<0.001, df= 8, n= 9), such that the rank order from highest to lowest was Rest in Contact > Approach > Follow > Close Sniff > Evade > Body Rub > Groom > Swipe > Cheek/Head Rub. Again, the rank order is provided to give some indication of the extremes, e.g. the low rates of some contact and aggressive actions, but do not imply a significant difference between individual elements. As explained before, the Friedman's test statistic and probability level refer to the group as a whole, and the result should be interpreted with care. Median values are shown in Figure 4.5.c.

As for the more rare activities, Juveniles showed a modicum of Social Play, initiating 12% of the total observations, mainly toward Adults (62%). This was only slightly more than the amount of Play seen initiated by Adults to others, and perhaps indicates that the high levels of Play observed in Kittens tail off sharply and then continue at some low level through Juvenile and Adult life. Object Play was similar to Adult levels (47% of the total), and was performed more by Males (Male n=36, Female n=11), and seldom involved prey animals. Juveniles showed little active mating behaviour until they reached maturity (and became "Adults"), except to grapple with other Juveniles and Kittens (n=27) and as rather unwilling subjects of Mount attempts (n=42) when all data were included. Juveniles initiated 22% of all Paw actions and received 19% (mainly with Adult Females).

Juveniles contributed only 10% of all Ear Flattening, most of which was nonspecific (96% of the Ear Flattening total for Juveniles), and 20% of all Tail Lashing, again mainly nonspecific (81% of the Tail Lashing total for Juveniles). Only once was a Juvenile seen to Piloerect (4% of all Piloerection), and this was to an Adult Female. Until Juveniles started to show mature behaviour such as Spray-Marking and Mounting, they were relatively undisturbed by Fights; Females continued to show low levels of Fighting after they matured, unlike the original Adult Females. Juveniles seldom Bit others (n=1) and were rarely Bitten by others (n=2). Juveniles were never seen to Nurse Kittens. As for Scratching, Juveniles did markedly less than Adults (27% of the total), whether considered from Focal or Occasional observations. Rolling (Figure 4.4.b), as briefly mentioned earlier, was frequently performed by Juvenile Males (35% including matured 1988 Kittens) and Females (27%), although less was received by these Juveniles (Males: 7%, Females: 5%). High levels occurred in February to April in both 1988 and 1989, during gestation and breeding periods. Juvenile Males Rolled equally to both Adult Males and Females, while Juvenile Females Rolled primarily to Adult Males (83%).

4.2.4. KITTEN RELATIONSHIPS

The suckling of Kittens was one of the main forms of Female-Kitten interaction. A total of 1929 intervals (16 hours) were recorded for Nursing, including both the suckling of a cat's own Kittens and allosuckling. Over all Females, 46% of Nursing was directed to own Kittens, and the rest was to communal or other Kittens. This ratio varied for the two groups; on Side A, 66% involved Females and their own Kittens (jumping up to 89% if the suckling of an abandoned and later adopted Kitten was included), while Side B Females suckled their own litters for only 32% of the observations (and suckled the kittens of other mothers for the remaining 68% of Nursing observations). Side B observations were heavily biased by the presence of Jenny, who allonursed after the

loss of her own litter. Other individual differences in Nursing are explored in Section 4.3.6, where litters are treated as units for the purpose of comparing own versus other Kittens.

Kittens contributed the majority of Social Play observations (78%), primarily with Adults. Only 2% of all Play was initiated toward Kittens by Adults and Juveniles; there was no way (practically or retrospectively) to measure Play levels between Kittens, as they were non-focal individuals, who moved quickly and invisibly through the long grass of the enclosure. Roughly, Kittens were seen to Play much of the time from the age of five weeks through to three or four months old; more detailed accounts of Kitten Play have been offered by authors working with more manageable numbers in controlled spaces (Barrett & Bateson 1978; Bateson 1981; Bateson & Young 1981; Martin 1982; Mendl 1986).

Adult-Kitten interactions were also examined for the nine common activities. Females were tested for differences in the levels of initiation toward their own and other Kittens, but no significant differences were found (Table 4.4). When all Females and Kittens were included, different activities were performed at different levels using a Friedman's test, with each activity as a "block" entry matched for the identity of recipient, e.g. own or other Kittens (χ_r^2= 148.449, $p<0.001$, df= 7, n= 77), such that the ranks were: Rest in Contact > Groom > Close Sniff > Evade > Approach > Swipe > Body Rub > Follow. When Females were considered with only their own Kittens across all activities, the results were similar (χ_r^2= 74.374, $p<0.001$, df= 7, n= 36); Females considered with other Kittens (not their own) also showed few changes (χ_r^2= 76.729, $p<0.001$, df= 7, n= 41). Thus Females acted more or less without regard to the identity of the Kittens, but appeared to Body-Rub and Evade their own Kittens a bit more, relative to other Kittens. As before, the rank order is provided to give some idea of the elements at the extremes, but does not imply significant differences between any two activities.

4.2.5. VOCALISATIONS

Accurate recording of vocalisations was problematic, given the open nature and size of the enclosure, and was hindered by observations taken from inside the "tower" (e.g. muffled sound). As a result, vocalisation has been treated broadly, and conclusions were drawn from individual and group level, and not examined as a specific dyadic feature. Meow, Yowl and Call were pooled, as were Brrr and Purr, Hiss and Growl, in an attempt to create separate functional categories (e.g. general, amicable and agonistic respectively). More Meows were recorded for Group B, more Yowls for A, and roughly equal numbers of Calls. Males contributed the majority of Yowls (75%), Females Meowed most (87%), and Calls were approximately equal (Females: 46%). It is likely that these differences

Table 4.4: Differences in Actions by Females Toward Own and Other Kittens (n=36,41). A significant result would mean that Females initiate the behaviour pattern at a different rate, depending on the identity of the Kitten.

Behaviour	**U**	**Z**	**p**
Follow	722.5	- .472	.637
Approach	691.5	- .780	.435
Evade	611.5	-1.675	.094
Cheek/Head Rub †	738	0	1
Body Rub	709.5	- .681	.496
Close Sniff	679	- .699	.485
Groom	647.5	-1.009	.313
Swipe	737	- .016	.988
Rest in Contact	646	-1.034	.301

(† no observations)

indicate a division of functions for each of these sounds, with Yowling playing a role in Male courting and territorial threat, Meows being used for communicating to Kittens and others, and Calls as another form of mating communication. Many of the vocalisations were made with no obvious recipient, both by Juveniles and by Adults

Brrr and Purr were very rare, and were almost all performed by cats in Group B; Males made the Brrr sound to Females (28%) and Females to Kittens (20%), and just under half involved Juveniles. One particular occasion provided 97% of the Purr observations, by a Female (Wanda) to a Male (Zac). It is very possible that the majority of these sounds were not recorded, as they are both quiet and can easily occur without being heard by a human observer; Females are generally known to purr frequently when suckling, but this did not contribute to the data in the study.

Side B cats Growled and Hissed more in general (66% of the total intervals); Adults, particularly Females, directed agonistic vocalisations to other Adults (50%), and Kittens (38%), especially to those Kittens not their own. Juveniles (especially "Juvenile" Males) appeared to Hiss and Growl most at Adult Males (75%). These sounds are probably used as threat and can be shown when either aggressive or defensive.

4.2.6. COLONY SUMMARY

The two groups showed no major differences regarding social behaviour patterns in Adults. Males tended to Follow and Close Sniff Females, Females Evaded and Swiped Males, and Females were affiliative (e.g. Approach, Rubbing, Grooming and Resting in Contact) with other Females. The Juveniles in the two groups showed some differences in activity rates.

Generally, Adult Males initiated activities that could be attributed to mating, whilst they received affiliative and agonistic behaviour from Adult Females. Adult Females displayed both maternal behaviour and affiliative social relationships with other Adult Females. Juveniles mainly interacted with Adults, although they were seen to Groom and Rest in Contact predominantly with Kittens. Females apparently directed actions toward Kittens without regard to their specific identity, but Body-Rubbed and Evaded their own Kittens more than they did other Kittens.

The less common activities included the following results: Adult Females and Kittens initiated most Paws; Ear Flattening and Tail Lashing were usually performed by Adults, especially Females, and had no apparent recipient for most occasions, and were seen in both conflict and non-conflict situations; Piloerection was performed solely by Females, and usually had no obvious recipient; Adult Females and Juveniles showed the most Object Play; Females Scratched objects more than did Males; Adults did most of the Mounting, and Juveniles were not seen to Mount Adult Females; Males occasionally

Mounted inappropriate subjects, although most of the recipients of attempts were Adult Females; Biting was rare, and was seen both in mating and agonistic contexts; Kittens performed most of the Subject Play; Males Yowled more, while Females Meowed more, with both vocalisations having no obvious recipient; and Females Hissed/Growled at other Adults and Kittens, while Juveniles Hissed/Growled mainly at Adult Males.

There was some indication that Rolling was not just involved in Female-Male interactions, but may also be some form of submission or appeasement behaviour (as seen in some canids), as suggested by the substantial proportion of Rolls directed by Juvenile Males to Adult Males.

4.3. THE DYAD

The hourly rate at which each behaviour pattern was performed was calculated for each dyad, giving a total of 301 combinations. These rates were then subjected to correlation analysis, across all dyads and over all Focal Females, in order to pinpoint associations between the rates of different activities performed with specific dyadic partners. The overall results are given in Table 4.5.a. Individuals differed in the subset of correlated patterns, although general trends were apparent; another difference lay between the associated rates for actions initiated and those received (Table 4.5.b). Chi-Square tests were performed to look at the significance of asymmetry (on the raw data values), comparing the behavioural initiations by each individual in Adult-Adult dyad combinations, but the technique was limited by the presence of small sample numbers (e.g. less than 5); all possible results are presented, with additional reference to untestable examples.

In the following sections, Figure 2.2 can be used as a reminder of the individuals in each group and their relatedness to other named members of the group.

4.3.1. FEMALE-FEMALE INTERACTIONS

Social interactions were arranged in a complex fashion among the various Adult Females of each group. No asymmetry was found for Follow or Swipe; however, Approach, Evade, Rubbing, Sniffing and Grooming showed directional imbalance for certain dyads (Table 4.6). The overall results are shown in Figures 4.6.a-d, including the roles of Males. Katrina and Poppy, Becky and Tessa, Jenny and Molly, and Calico and Wanda show obvious dichotomies in behaviour initiated and received; interestingly, these same dyads were communal breeders at some time, with the exception of Jenny and Molly (who displayed intense amiable interactions together). In particular, Poppy Followed, Approached, Rubbed, Sniffed and Groomed Katrina more; other actions were given at

Table 4.5.a: The Results of Spearman Correlation Analysis Between Separate Behaviour Patterns (over all dyads, n=301). A significant result means that the (ranked) rates of the two behaviour patterns are linearly related.

Behaviour 1	Behaviour 2	r_s	Z	p	
Follow	Approach	.546	9.466	<0.001	***
Follow	Evade	.239	4.144	<0.001	***
Follow	Cheek/Head Rub	.278	4.816	<0.001	***
Follow	Body Rub	.270	4.674	<0.001	***
Follow	Close Sniff	.366	6.332	<0.001	***
Follow	Groom	-.129	-2.243	<0.05	*
Follow	Swipe	.314	5.433	<0.001	***
Follow	Rest/Sleep Contact	.126	2.189	<0.05	*
Approach	Evade	.391	6.767	<0.001	***
Approach	Cheek/Head Rub	.359	6.220	<0.001	***
Approach	Body Rub	.394	6.827	<0.001	***
Approach	Close Sniff	.493	8.533	<0.001	***
Approach	Groom	-.114	-1.981	<0.05	*
Approach	Swipe	.316	5.474	<0.001	***
Approach	Rest/Sleep Contact	.400	6.932	<0.001	***
Evade	Cheek/Head Rub	.138	2.390	<0.05	*
Evade	Body Rub	.236	4.088	<0.001	***
Evade	Close Sniff	.295	5.107	<0.001	***
Evade	Groom	.020	.342	.733	
Evade	Swipe	.271	4.692	<0.001	***
Evade	Rest/Sleep Contact	.234	4.054	<0.001	***
Cheek/Head Rub	Body Rub	.450	7.797	<0.001	***
Cheek/Head Rub	Close Sniff	.381	6.592	<0.001	***
Cheek/Head Rub	Groom	.065	1.121	.262	
Cheek/Head Rub	Swipe	.235	4.066	<0.001	***
Cheek/Head Rub	Rest/Sleep Contact	.195	3.377	<0.001	***
Body Rub	Close Sniff	.325	5.622	<0.001	***
Body Rub	Groom	.072	1.255	.209	
Body Rub	Swipe	.050	.860	.390	
Body Rub	Rest/Sleep Contact	.231	4.005	<0.001	***
Close Sniff	Groom	.278	4.810	<0.001	***
Close Sniff	Swipe	.288	4.986	<0.001	***
Close Sniff	Rest/Sleep Contact	.349	6.040	<0.001	***
Groom	Swipe	-.029	- .494	.621	
Groom	Rest/Sleep Contact	.387	6.710	<0.001	***
Swipe	Rest/Sleep Contact	.201	3.489	<0.001	***

Table 4.5.b: Individual Correlations for Focal Behaviour Rates (To others / By others)

Behaviour 1&2	JEN	CAL	WAN	MOL	DAI	KAT	BEC	TES	POP
Foll-Appr	+/+		+/		/+		+/		+/
Foll-Evade			+/				/+		+/
Foll-C/H/Rub	+/			+/		+/			+/
Foll-B/Rub	+/		+/			+/		+/+	+/
Foll-C/Sniff			+/	+/	/+				
Foll-Groom									
Foll-Swipe		/+		+/		+/			+/
Foll-Rt/Sl/C			+/	+/					
Appr-Evade	+/		+/			+/		/+	+/
Appr-C/H/Rub	+/							+/	+/
Appr-B/Rub	+/	+/	+/						+/
Appr-C/Sniff	+/	/+		/+	/+	+/+	/+	+/	+/
Appr-Groom			-/	-/			-/		
Appr-Swipe						+/			+/
Appr-Rt/Sl/C	+/		/+	+/				/+	+/
Evade-C/H/Rub			+/		+/				+/
Evade-B/Rub			+/				+/		+/
Evade-C/Sniff	+/		+/					/+	+/
Evade-Groom									
Evade-Swipe	+/		/+			+/			
Evade-Rt/Sl/C	+/		+/			+/			
C/H/Rub-B/Rub		+/	+/+			+/			+/
C/H/Rub-C/Sniff	+/			+/				+/	+/
C/H/Rub-Groom				/+		/+			
C/H/Rub-Swipe		+/							
C/H/Rub-Rt/Sl/C									
B/Rub-C/Sniff	+/	+/		+/				+/	+/
B/Rub-Groom			/+						
B/Rub-Swipe									
B/Rub-Rt/Sl/C	+/						+/		
C/Sniff-Groom		+/	/+	+/		+/			
C/Sniff-Swipe	+/		+/						/+
C/Sniff-Rt/Sl/C	+/		+/+						
Groom-Swipe									
Groom-Rt/Sl/ C	+/	+/				+/		+/	+/
Swipe-Rt/Sl/C									

Table 4.6: Chi-Square Tests for Differences in Dyadic Behaviour (df=1). For example, Trossachs Follows Pansy significantly more than Pansy Follows Trossachs.

Initiator	Recipient	Behaviour	χ^2	p	
Trossachs	Pansy	Follow	17.053	<0.001	***
Trossachs	Poppy	Follow	22.242	<0.001	***
Zac	Wanda	Follow	5.436	<0.05	*
Trossachs	Katrina	Approach	50.422	<0.001	***
Trossachs	Becky	Approach	20.056	<0.001	***
Trossachs	Tessa	Approach	28.373	<0.001	***
Pansy	Trossachs	Approach	46.723	<0.001	***
Trossachs	Poppy	Approach	36.834	<0.001	***
Poppy	Katrina	Approach	54.974	<0.001	***
Becky	Tessa	Approach	39.977	<0.001	***
Becky	Poppy	Approach	4.143	<0.05	*
Tessa	Poppy	Approach	4.955	<0.05	*
Zac	Jenny	Approach	32.866	<0.001	***
Calico	Zac	Approach	30.445	<0.001	***
Wanda	Zac	Approach	38.843	<0.001	***
Zac	Molly	Approach	5.062	<0.05	*
Calico	Jenny	Approach	15.743	<0.001	***
Wanda	Jenny	Approach	26.724	<0.001	***
Jenny	Laura	Approach	5.890	<0.05	*
Molly	Jenny	Approach	57.311	<0.001	***
Wanda	Calico	Approach	13.500	<0.001	***
Calico	Laura	Approach	4.530	<0.05	*
Wanda	Laura	Approach	.100	.752	
Trossachs	Tessa	Evade	7.778	<0.01	**
Pansy	Trossachs	Evade	4.978	<0.05	*
Poppy	Trossachs	Evade	8.912	<0.01	**
Zac	Wanda	Evade	1.730	.188	
Zac	Laura	Evade	.225	.635	
Jenny	Molly	Cheek/Head Rub	.111	.739	
Molly	Jenny	Body Rub	41.576	<0.001	***
Trossachs	Pansy	Close Sniff	3.771	.052	
Poppy	Katrina	Close Sniff	15.300	<0.001	***
Jenny	Zac	Close Sniff	6.769	<0.01	**
Zac	Calico	Close Sniff	.364	.547	
Zac	Wanda	Close Sniff	9.142	<0.01	**
Jenny	Molly	Close Sniff	4.077	<0.05	*

Figure 4.6.a

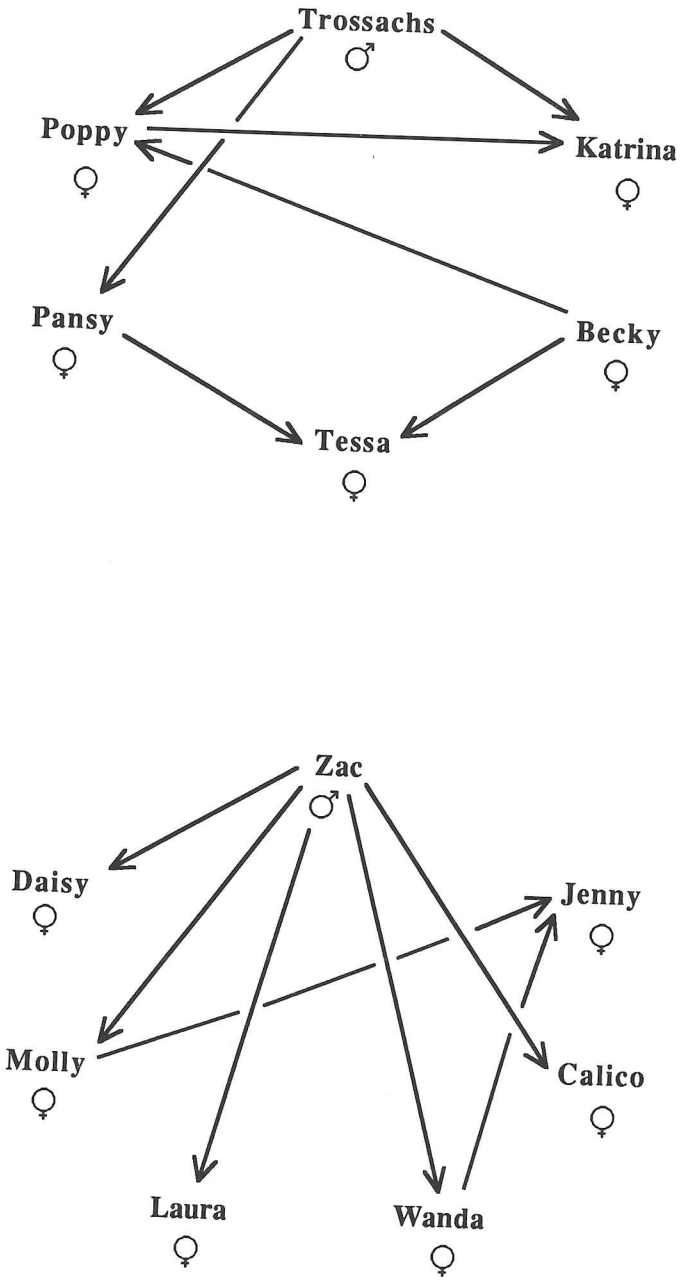
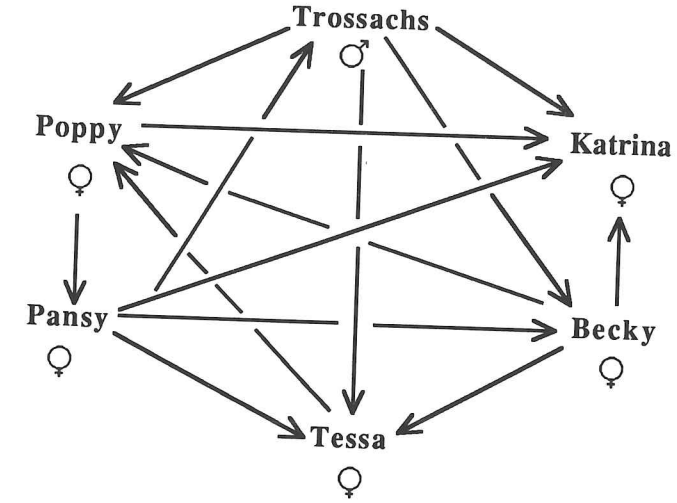


Figure 4.6.a: Asymmetry in Following between Adult dyad members. Values are based on Focal interval frequency, and have been analysed with χ^2-tests where cell frequencies were sufficiently large. The direction of the arrows shows the direction of the asymmetry, from the larger initiator to recipient. The top shows Group A and the bottom is Group B.

Figure 4.6.b



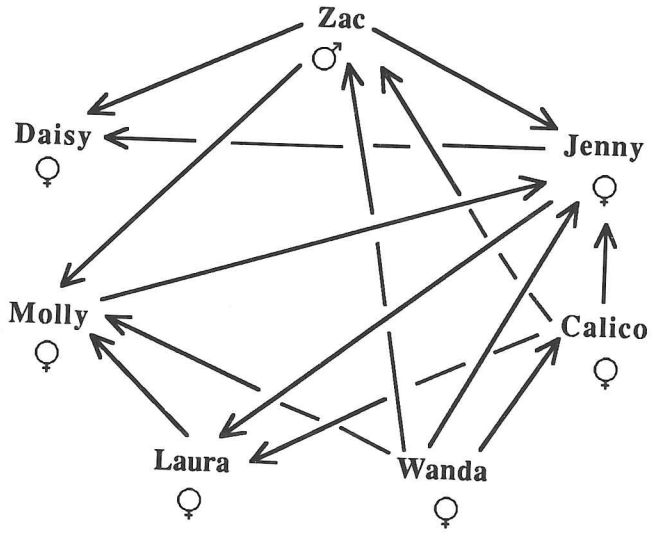


Figure 4.6.b: Asymmetry in Approaching between Adult dyad members. Values are based on Focal interval frequency, and have been analysed with χ^2-tests where cell frequencies were sufficiently large. The direction of the arrows shows the direction of the asymmetry, from the larger initiator to recipient. The top shows Group A and the bottom is Group B.

Figure 4.6.c

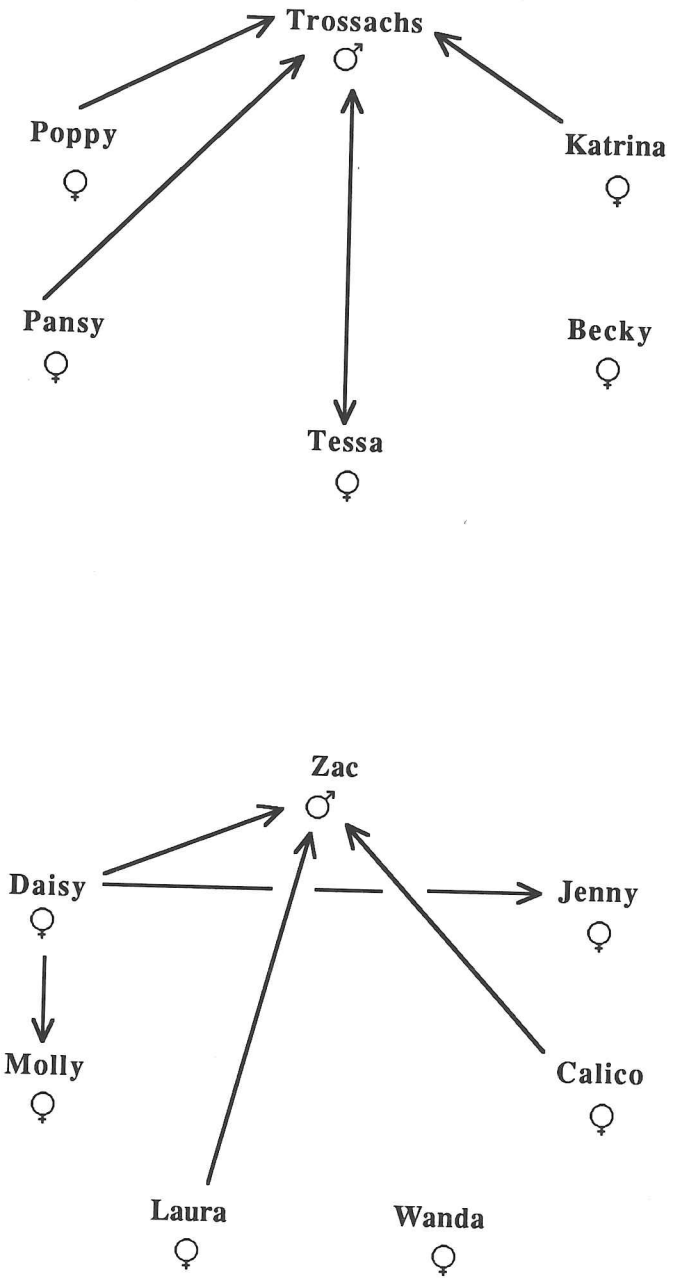


Figure 4.6.c: Asymmetry in two Agonism measures (Evading and Swiping) between Adult dyad members. Values are based on Focal interval frequency, and have been analysed with χ^2-tests where cell frequencies were sufficiently large. The direction of the arrows shows the direction of the asymmetry, from the larger initiator to recipient. The top shows Group A and the bottom is Group B.

Figure 4.6.d

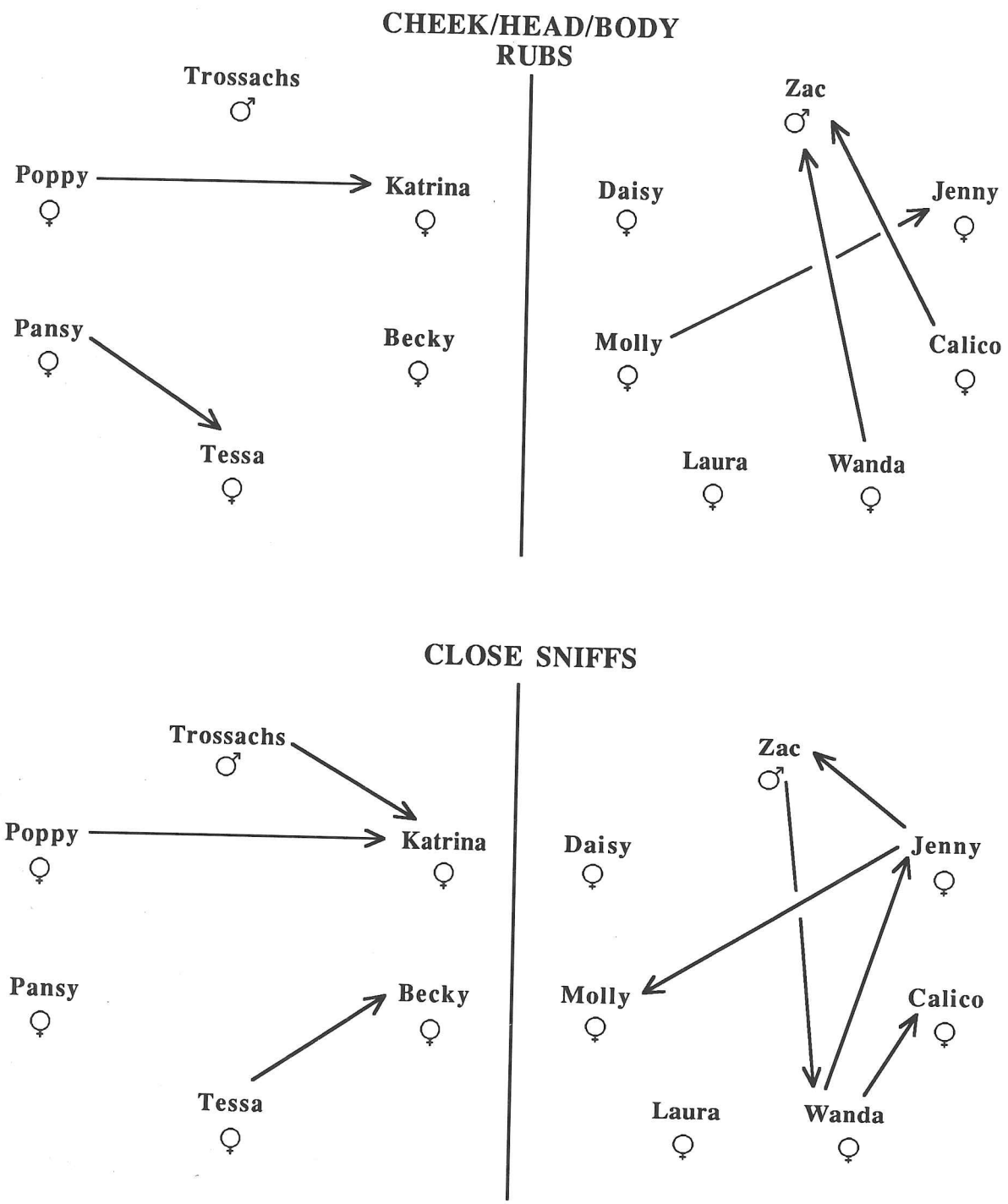


Figure 4.6.d: Asymmetry in Affiliative measures between Adult dyad members. Values are based on Focal interval frequency, and have been analysed with χ^2-tests where cell frequencies were sufficiently large. The direction of the arrows shows the direction of the asymmetry, from the larger initiator to recipient. The left shows Group A and the right is Group B.

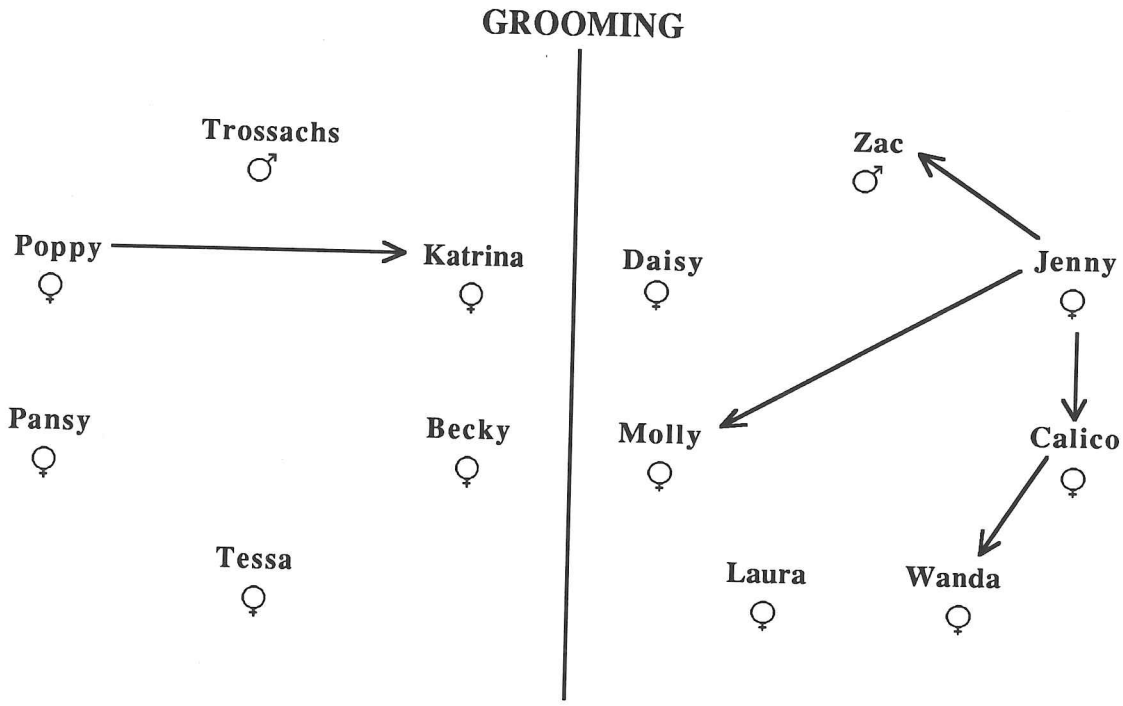


Figure 4.6.d (cont.): Asymmetry in Grooming between Adult dyad members. Values are based on Focal interval frequency, and have been analysed with χ^2-tests where cell frequencies were sufficiently large. The direction of the arrows shows the direction of the asymmetry, from the larger initiator to recipient. The left shows Group A and the right is Group B.

mutual levels. Becky Followed, Approached and Body-Rubbed Tessa, who Cheek Rubbed Becky; again, other actions were mutual. Wanda Followed, Approached and Sniffed Calico, who Groomed Wanda. All three of these combinations showed no Evade or Swipe.

Based on this result, the relationships between mothers and helpers (or "aunts") were also examined, as well as dyads who were past partners, or future ones. Poppy and Becky, who cooperated in 1987 and 1989, showed little directional interaction, although Becky preferred to Follow Poppy of all cats, and Approached Poppy more. Tessa and Poppy shared an ill-fated litter in 1989; Tessa tended to Approach Poppy, who Followed Tessa more. Molly was helped by Laura in 1987 and 1989, but the pair showed differences in initiation of Approach only, as was true for Calico and Molly, who pooled litters in 1987. Wanda, who was a co-helper with Laura in 1987, Groomed Laura more.

When "preferred" partners were examined, still more specific sets of relationships were found between the Females, which elucidated on the asymmetry of some dyadic relationships; if each pair is described separately, trends can be seen. Poppy Followed and Rubbed Katrina, they Approached Sniffed, Groomed and Rested with one another; generally, Poppy appears to have made most of the overtures, which were treated amicably. Becky Followed Tessa, Tessa Groomed Becky, and they Rubbed, Sniffed and Rested with each other; this dyad seemed to have a slightly more reciprocal maintenance of amiability. As for cooperative dyads from past and future litters, Tessa Rubbed Poppy, who Swiped her "in return" (although not necessarily during the same encounter); the unease of the relationship may foreshadow and reflect the difficulties these females had in cooperation (they abandoned a pooled litter in 1989; see Section 5.5.5). Becky Followed Poppy, who later helped Becky after the loss of her own litter in 1989. As for Pansy, who failed to breed and appeared somewhat peripheral to the group, she generally preferred Trossachs and Tessa, although Rested most with Becky.

In Group B, Calico Groomed Wanda, who preferred to Rest with Calico; most other behaviour was directed to others. Calico did not interact primarily with Molly (a past partner), but Rested more with Laura (a past helper). Wanda mainly focussed on Laura (a past co-helper) and Jenny. Molly and Laura shared no preferences either, despite Laura's helper role in 1987 and 1989. Laura divided her attention between Zac, Wanda and Jenny. Daisy, another apparently peripheral Female, interacted much less, although she "preferred" Zac (Close Sniff) and Wanda (Follow and Approach); the only marked responses were more agonistic, and were directed to Zac and Jenny.

4.3.2. FEMALE-MALE INTERACTIONS

The two Adult Males were significant initiators of Follow and Approach behaviour to most Females, with Poppy and Katrina receiving from Trossachs, and Jenny and Molly receiving from Zac. Both Males received significantly more Evasion and Swiping from Females than they performed toward the Females; occasionally, they also had asymmetric pro-social interactions, but these were less likely to be significant due to the paucity of Male initiations in this area. By far the clearest examples of Female-Male directionality were posed by Follow and Approach, two apparently investigative actions that were likely associated with mating. Males did appear to prefer particular Females; observed Mounts were on Poppy and Katrina for Trossachs, echoing his initiation of other behaviour patterns. However, Jenny and Molly were not the more frequent subjects of Zac's Mount attempts; on the other hand, he received more amiable attention from those two Females, and the Follow and Approach levels may have reflected social rather than reproductive factors.

Between any Female and the resident Adult Male, a typical imbalance was observed; the Male Approached, Followed and Close Sniffed more, while the Female Evaded and Swiped more. Undoubtedly, this was an outcome of the tensions surrounding mating, with the Male frequently investigating and testing the Female, and receiving her agonistic reactions when enacted outside of the brief window of Female sexual receptivity. Relatively little non-reproductive behaviour (e.g. the so-called affiliative actions) was exchanged between Adult Females and Males. This was particularly true with Trossachs, who spent long periods alone, patrolling the boundaries of the enclosure.

Analysis of "preferred" partners for actions further elucidated the trends indicated by the comparison of directionality within each Adult dyad. The frequency of intervals was expressed as a proportion of the total from each Focal animal over each behaviour. These were then summarised in diagram form (Figures 4.6.e-m). Net initiators included Trossachs, Becky and Zac for Follow, Trossachs and Zac for Approach, Tessa and Katrina for Cheek Rub, Pansy and Zac for Close Sniff, Poppy and Zac for Swipe, and Zac and Jenny for Groom. Net Recipients were Katrina, Poppy and Jenny (Follow), Tessa, Trossachs, Zac and Jenny (Approach), Trossachs and Zac (Evade), Poppy, Zac and Jenny (Cheek Rub), Tessa and Zac (Body Rub), Katrina and Zac (Close Sniff), Trossachs and Zac (Swipe), and Zac and Calico (Groom). The notable feature was the involvement of Males as common partners for many activities, and their presence as initiators to Females.

Figure 4.6.e

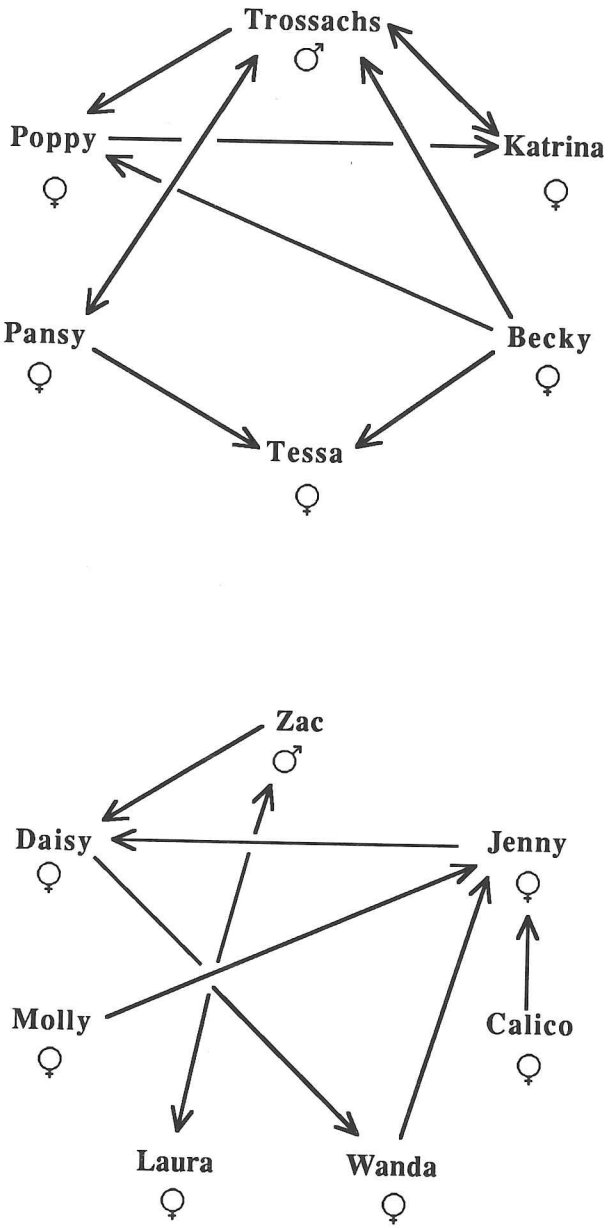


Figure 4.6.e: "Preferred" partners for Adult-Adult behaviour: **Following**. Values are based on Focal interval frequency as a proportion of the total initiated by each Focal individual Only scores greater than random are shown Arrows are directed from each Focal cat to its most common partner. Where an animal has more than one arrow origin, values were tied. The top diagram is Group A and the bottom is Group B.

Figure 4.6.f

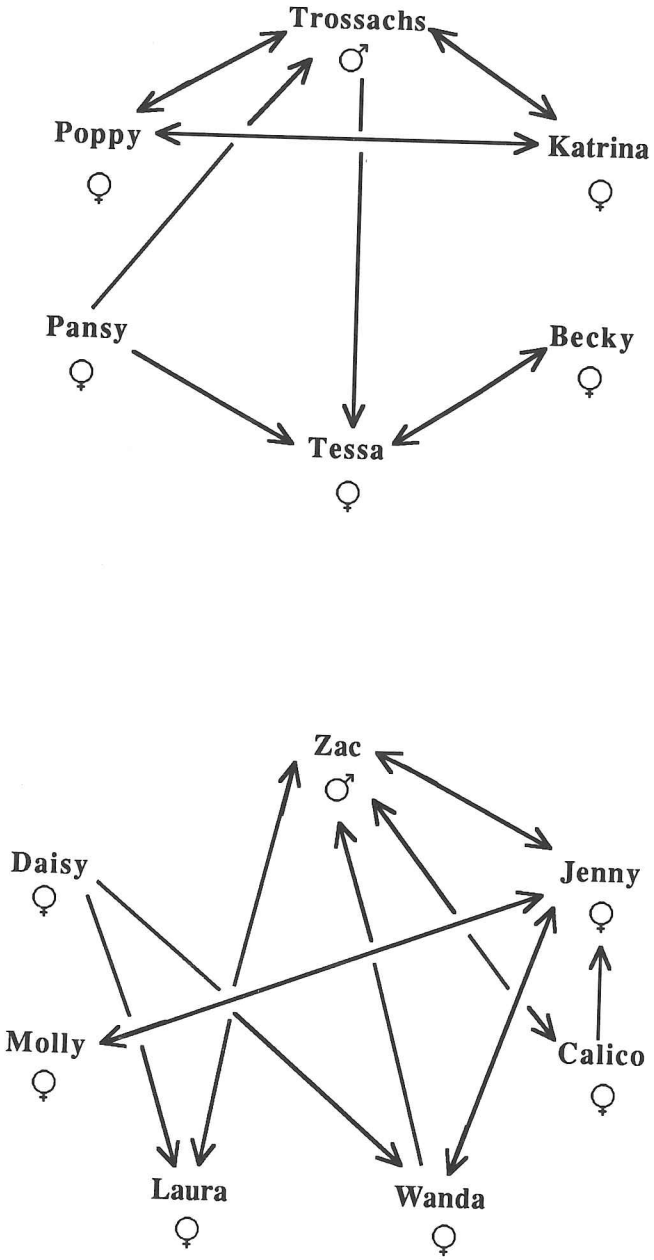


Figure 4.6.f: "Preferred" partners for Adult-Adult behaviour: **Approaching**. Values are based on Focal interval frequency as a proportion of the total initiated by each Focal individual Only scores greater than random are shown Arrows are directed from each Focal cat to its most common partner. Where an animal has more than one arrow origin, values were tied. The top diagram is Group A and the bottom is Group B.

Figure 4.6.g

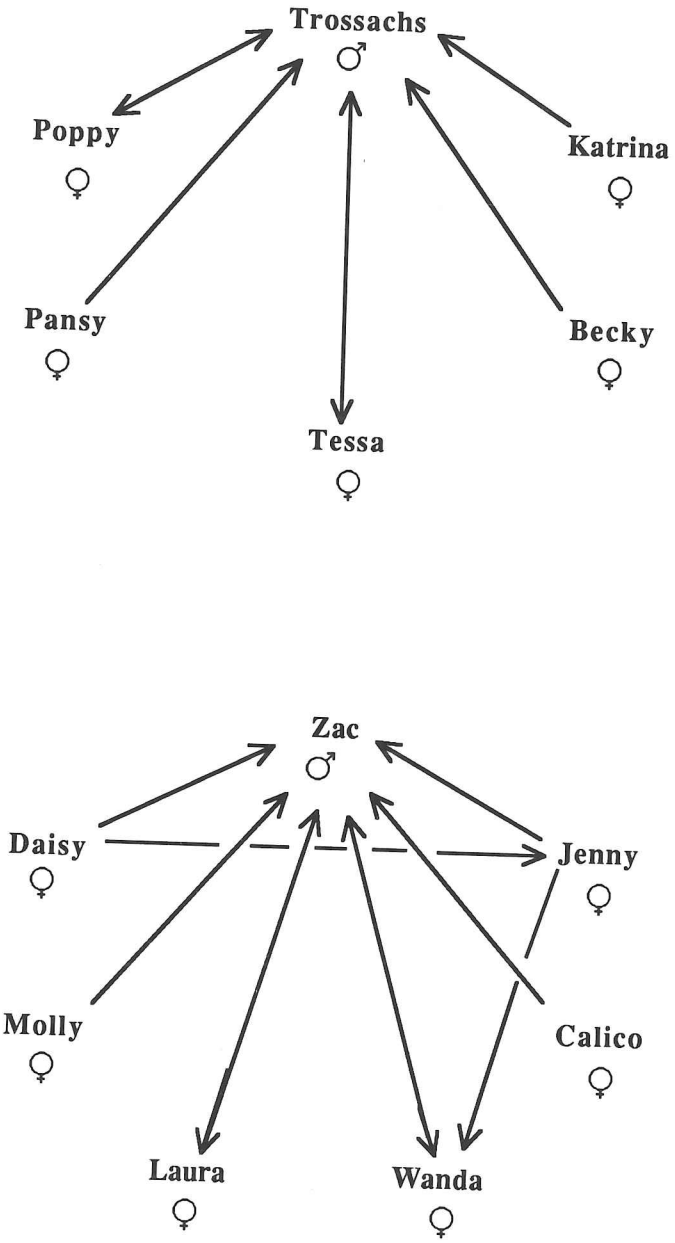


Figure 4.6.g: "Preferred" partners for Adult-Adult behaviour: **Evading**. Values are based on Focal interval frequency as a proportion of the total initiated by each Focal individual Only scores greater than random are shown Arrows are directed from each Focal cat to its most common partner. Where an animal has more than one arrow origin, values were tied. In this behaviour, arrows point from the cat who Evades to the individual it is Evading. The top diagram is Group A and the bottom is Group B.

Figure 4.6.h

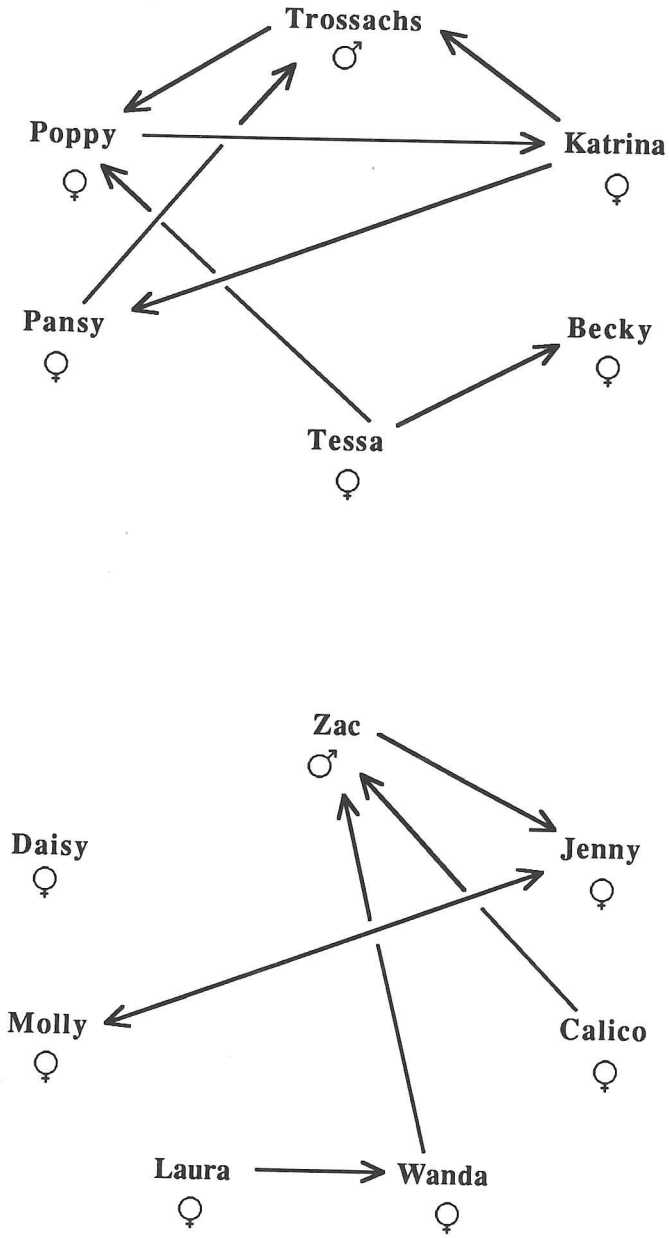


Figure 4.6.h: "Preferred" partners for Adult-Adult behaviour: **Cheek and Head Rubbing.** Values are based on Focal interval frequency as a proportion of the total initiated by each Focal individual Only scores greater than random are shown Arrows are directed from each Focal cat to its most common partner. Where an animal has more than one arrow origin, values were tied. The top diagram is Group A and the bottom is Group B.

Figure 4.6.i

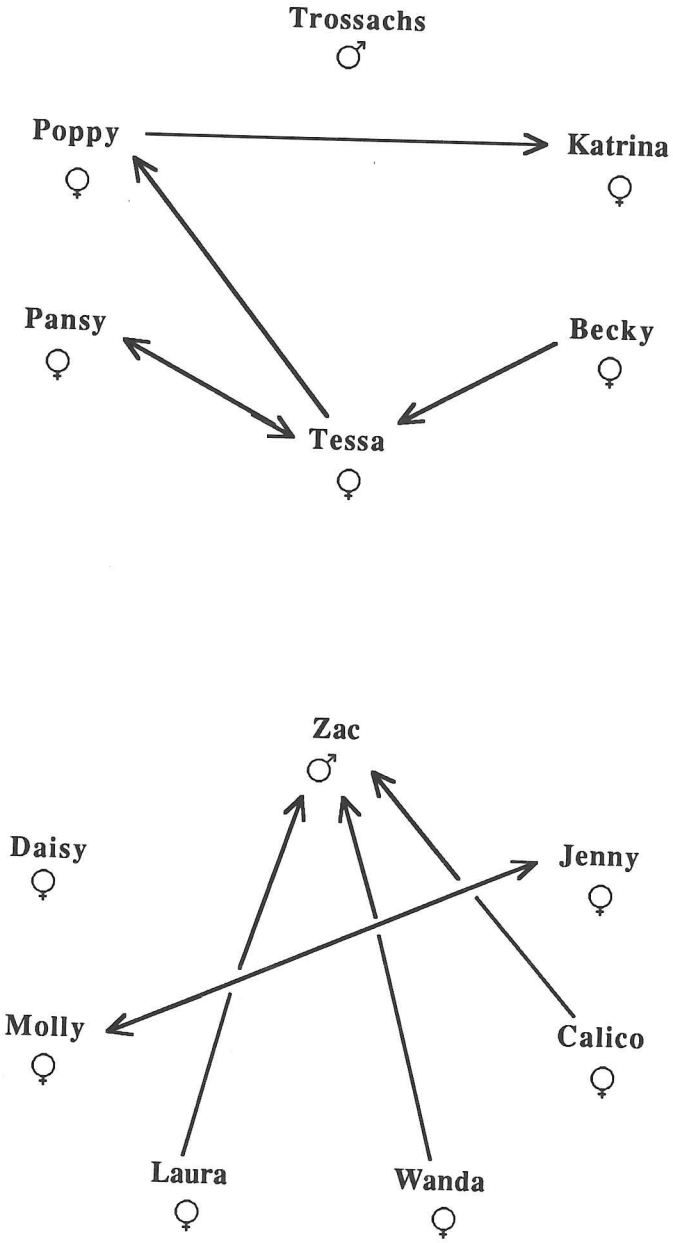


Figure 4.6.i: "Preferred" partners for Adult-Adult behaviour: **Body Rubbing**. Values are based on Focal interval frequency as a proportion of the total initiated by each Focal individual Only scores greater than random are shown Arrows are directed from each Focal cat to its most common partner. Where an animal has more than one arrow origin, values were tied. The top diagram is Group A and the bottom is Group B.

Figure 4.6.j

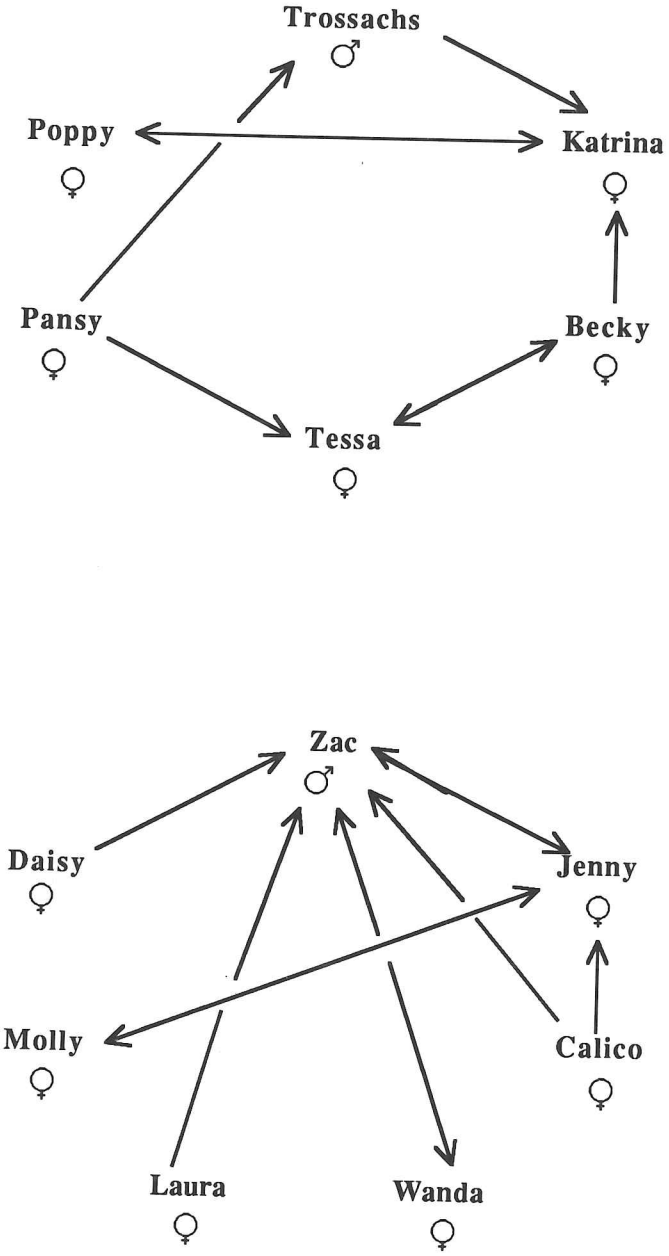


Figure 4.6.j: "Preferred" partners for Adult-Adult behaviour: **Close Sniffing**. Values are based on Focal interval frequency as a proportion of the total initiated by each Focal individual Only scores greater than random are shown Arrows are directed from each Focal cat to its most common partner. Where an animal has more than one arrow origin, values were tied. The top diagram is Group A and the bottom is Group B.

Figure 4.6.k

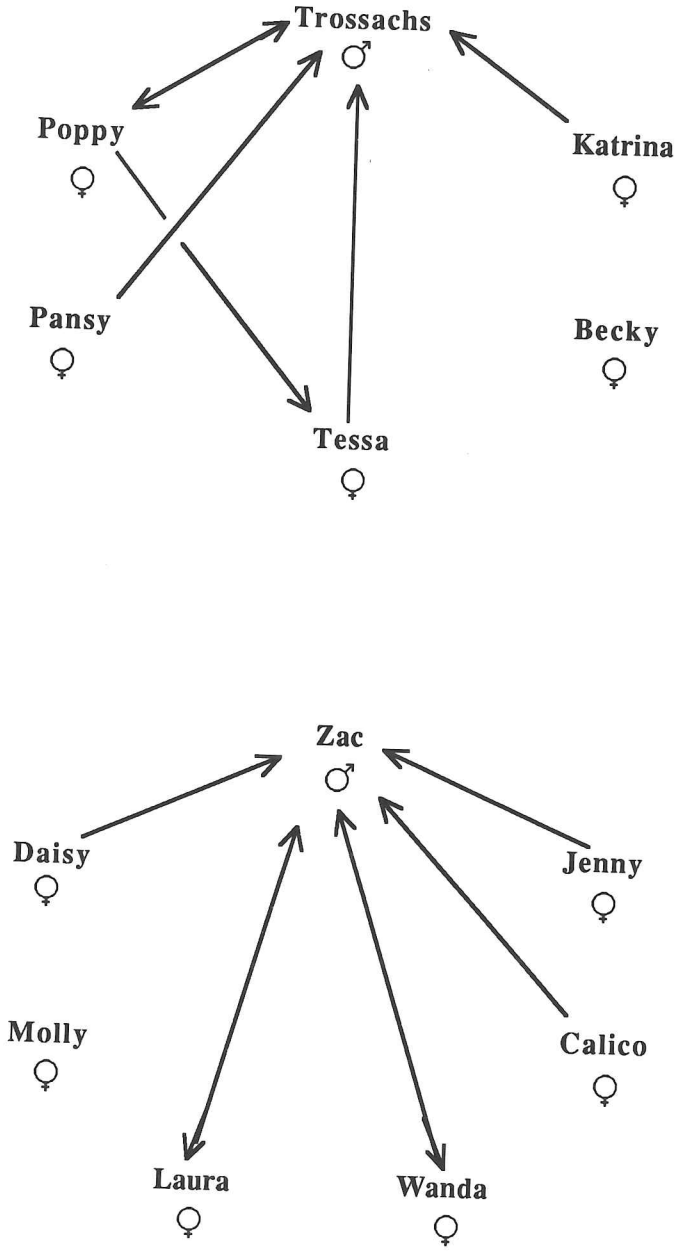


Figure 4.6.k: "Preferred" partners for Adult-Adult behaviour: **Swiping**. Values are based on Focal interval frequency as a proportion of the total initiated by each Focal individual Only scores greater than random are shown Arrows are directed from each Focal cat to its most common partner. Where an animal has more than one arrow origin, values were tied. The top diagram is Group A and the bottom is Group B.

Figure 4.6.I

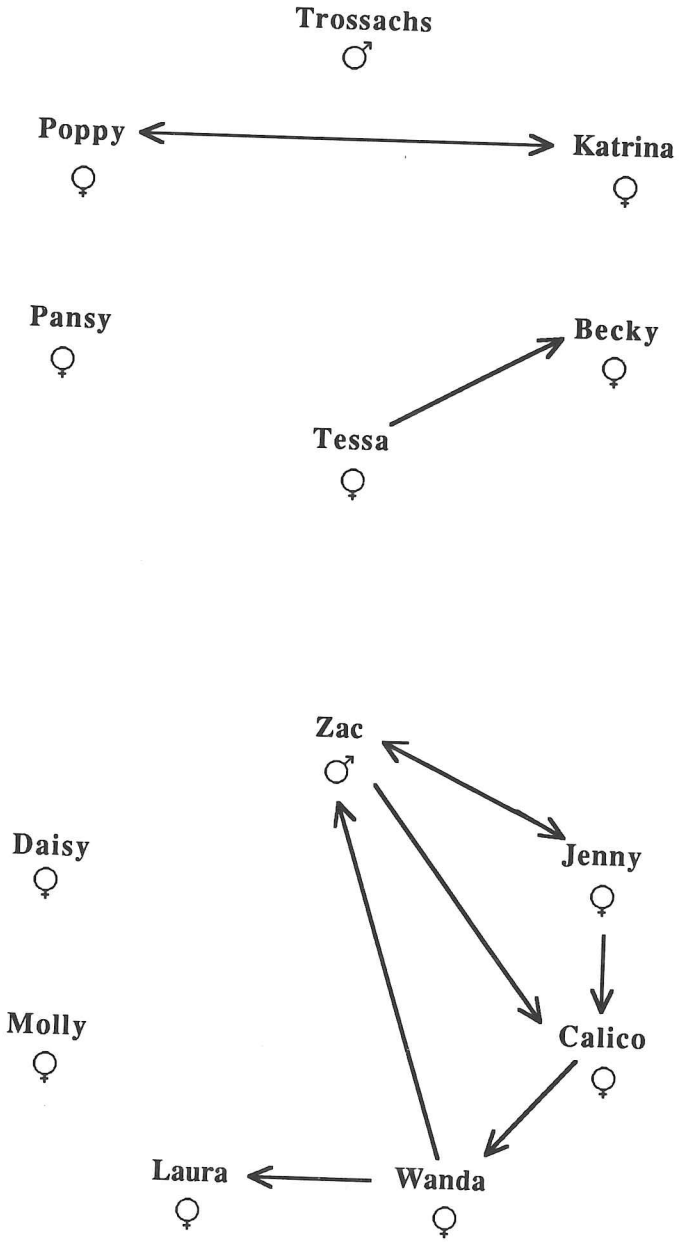


Figure 4.6.I: "Preferred" partners for Adult-Adult behaviour: **Grooming**. Values are based on Focal interval frequency as a proportion of the total initiated by each Focal individual Only scores greater than random are shown Arrows are directed from each Focal cat to its most common partner. Where an animal has more than one arrow origin, values were tied. The top diagram is Group A and the bottom is Group B.

Figure 4.6.m

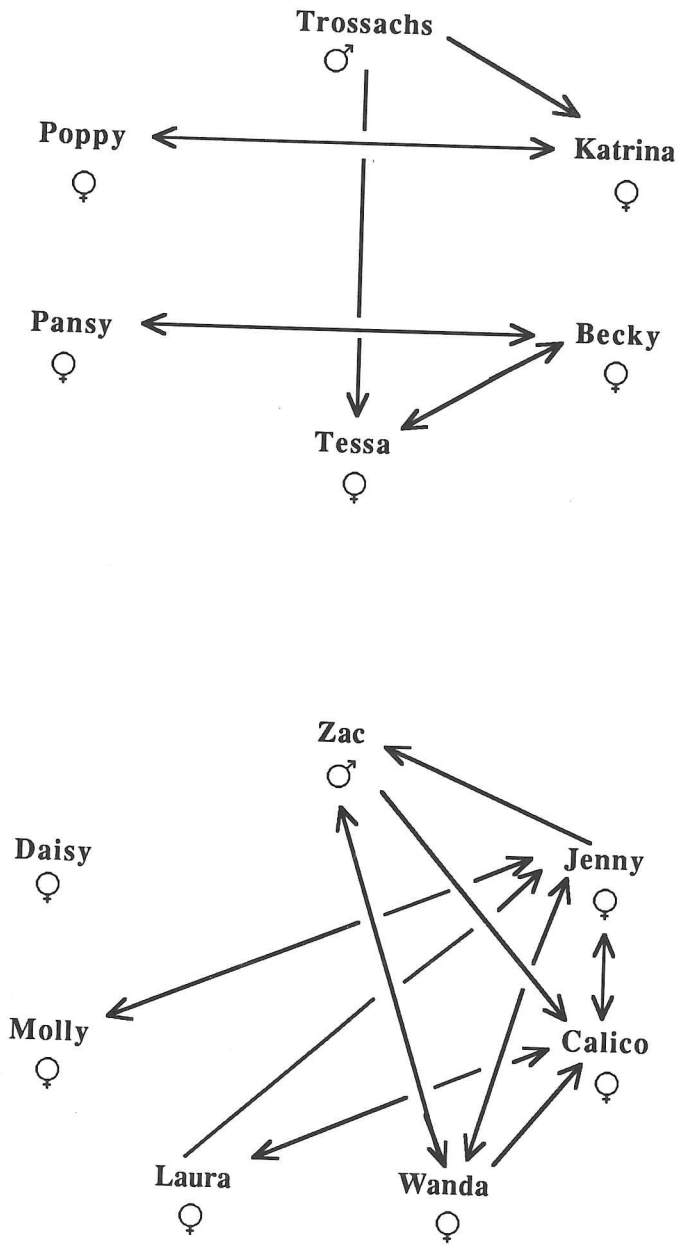


Figure 4.6.m: "Preferred" partners for Adult-Adult behaviour: **Resting and Sleeping in Contact.** Values are based on Focal interval frequency as a proportion of the total for each Focal individual Only scores greater than random are shown Arrows are directed from each Focal cat to its most common partner. Where an animal has more than one arrow origin, values were tied. The top diagram is Group A and the bottom is Group B.

4.3.3. MALE-MALE INTERACTIONS

For the most part, it was not possible to look at Adult Male-Male interactions, as the two groups were founded by a single Male each. A few encounters occurred across the separation boundary, but these were rare, and usually involved vocalisations and the occasional exchange of Swipes or Bites. Only after the maturation of Males born in 1987 were multiple Males present in any one group. For Group A, only the dyad Trossachs-Pishi was possible, whereas Group B included Zac as well as his sons, Carbonel, Catkin, Dijon and Doolittle. Most behaviour involved investigation and/or agonism; older Males Followed and Approached the newly matured Males, who often Evaded. Zac Ear Flattened and Tail Lashed at these "intruders", and Fights were common, as were Hissing and Growling vocalisations.

In fact, in the spring of 1989, despite the challenge of the fence barrier, most of the younger Males managed to emigrate. The prime individuals to "disperse" were Doolittle and Dijon, and later Carbonel; these Males were the main recipients of aggression from Zac, while Catkin received little due to his more solitary habits and his involvement with the rearing of a litter born to his mother. Pishi and Trossachs, while wary and somewhat avoidant of one another, managed to co-exist in the same group; Males from Side B were sometimes seen to take refuge in Side A, although they met with agonism from most of the group (especially Trossachs). The visits by young Males to the other side were rare and short, and so were unlikely to affect the stability of relationships within either group. When the younger Males occasionally returned to the enclosure, probably attracted to the availability of food and the concentration of Females, they were instantly chased and attacked by Zac, and invariably left immediately. There exists little doubt but that Zac would have followed and continued his aggression if he could have made the leap to the fence brim.

4.3.4. ADULT-JUVENILE INTERACTIONS

Male-Juvenile relationships are covered in earlier sections, such that Adult Males primarily directed investigative behaviour to Juveniles, with more mating interest for Females and agonism toward Males (also in Dards 1979). Females showed more variation in their actions to Juveniles. Katrina, Becky, Tessa and Poppy initiated most activities toward Bojangles, but Evaded and Swiped Brigit and Pippin; while Pansy "preferred" Brigit for amicable encounters. Carbonel and Catkin received the most amicable attention from Side B Females, with Molly and Laura focussing amicable initiations toward Mulberry, and Daisy mainly initiating actions to her son, Dijon. The aspect of relatedness and early experience appeared to play some role, especially with Group B, but individual

Juveniles undoubtedly forged their own interactions with other Females. A relationship between Adult Females may introduce Juvenile offspring to specific others, which, in turn, might predispose interactions with those more familiar Adults.

Side A Juveniles interacted frequently with Adults; the following section discusses "preferred" partners for each behaviour. These are summarised in Table 4.7. In general, Bojangles initiated actions to Katrina and Poppy (an allomother), except for the more agonistic Evade and Swipe, directed to the Male Trossachs. Brigit "preferred" Poppy (her allomother) except with Close Sniff, Swipe and Rest in Contact, which were mainly initiated to Trossachs. Pippin also favoured Poppy (her mother) and Katrina, but also Approached and Swiped Trossachs. Pishi directed to Katrina and Poppy (his mother), but Approached and Evaded Trossachs.

Side B Juveniles were more varied; Carbonel interacted mainly with Jenny and Laura (an "aunt") except for Evading (Wanda, an "aunt", and Zac), Close Sniff (Zac and Molly, his allomother), Groom and Rest in Contact (both with his mother, Calico). Catkin initiated mainly to Laura and Jenny, but Evaded and occasionally Groomed Zac; he also Rested quite a lot with Calico, his mother. Dijon was associated with Jenny for most behaviour, but Evaded and Swiped Zac (and Body Rubbed him, n=1); his mother, Daisy, received more Close Sniffs, and Calico was the favoured Resting partner. Doolittle mainly directed behaviour to Molly, and sometimes Calico, but the agonism of Evading and Swiping were usually reserved for Zac. The last Juvenile, Mulberry, often interacted with her mother, Molly, but also included Jenny (Approach) and Laura, an "aunt" (Cheek/Head Rub and Rest in Contact); the majority of Close Sniffs, Swipes and Evasion went to Zac (and Wanda - regarding Evade).

4.3.5. JUVENILE-JUVENILE INTERACTIONS

Juvenile-Juvenile interactions were less commonly observed, perhaps due to the compounding of shorter total periods of watches, and the reduced visibility of many Juveniles. As with Juvenile-Adult interactions, it was possible to find common partners for many activities, and these are described here. Bojangles typically initiated behaviour to Pippin and Pishi (her Female and Male communal littermates); Brigit interacted mainly with Pippin (Female communal littermate), but Evaded and Rested more with Pishi. The two supposed sisters, Bojangles and Brigit, exchanged relatively little behaviour, seeming to prefer the company of other littermates. As for Pippin and Pishi, Pippin often returned the preference of Bojangles and Brigit, but Cheek Rubbed, Close Sniffed and Swiped her brother. Pishi preferred Brigit, except for the Approaches and Sniffing, which were mainly given to Bojangles; Pippin was not ignored, but was not the preferred partner for any of the major Focal activities.

Table 4.7: Preferred Partners for Juvenile-Adult Behaviour

Juvenile	Follow	Approach
Bojangles	Katrina (40%),Poppy (39%)	Katrina (39%)
Brigit	Katrina (31%),Poppy (24%)	Poppy (26%)
Pippin	Poppy (36%),Katrina (31%)	Poppy (25%)
Pishi	Katrina & Poppy (37%)	Poppy (26%),Trossachs (23%)
Carbonel	Jenny (28%),Laura (22%)	Jenny (28%), Laura (22%)
Catkin	Laura (57%),Jenny (43%)	Jenny (28%)
Dijon	Jenny (31%)	Jenny (23%)
Doolittle	Molly (80%)	Molly (29%)
Mulberry	Molly (43%)	Jenny (27%)

	Evade	Cheek/Head Rub	Body Rub
Bojangles	Trossachs (50%)	Becky (100%)	Katrina (38%)
Brigit	Tessa & Poppy (33%)		Poppy (57%)
Pippin	Katrina (43%)	Katrina & Poppy (50%)	Poppy (33%)
Pishi	Trossachs (78%)		
Carbonel	Wanda (39%)	Jenny (33%)	Laura (45%)
Catkin	Zac (75%)		Jenny (100%)
Dijon	Zac (40%)		Zac (100%)
Doolittle	Zac (71%)		
Mulberry	Wanda (48%)	Laura (100%)	Molly (46%)

	Close Sniff	Groom
Bojangles	Katrina (43%)	
Brigit	Trossachs (27%)	
Pippin	Becky (40%)	
Pishi	Katrina & Poppy (33%)	
Carbonel	Zac & Molly (32%)	
Catkin	Jenny (67%)	Calico (100%)
Dijon	Daisy (32%)	Zac & Jenny (40%)
Doolittle	Laura & Molly (50%)	Jenny (100%)
Mulberry	Zac (60%)	

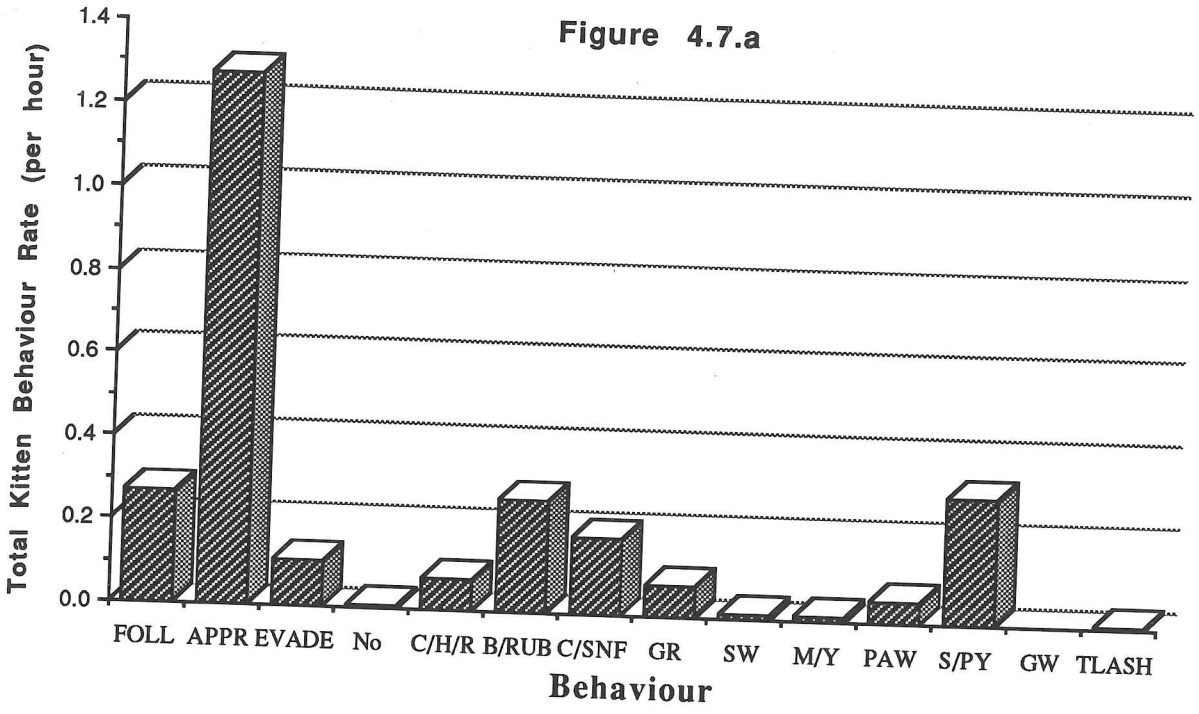
	Swipe	Rest/Sleep in Contact
Bojangles	Trossachs (100%)	Katrina (43%), Poppy (39%)
Brigit	Trossachs (100%)	Trossachs (100%)
Pippin	Trossachs (100%)	Katrina (73%)
Pishi		Katrina (100%)
Carbonel	Jenny (100%)	Calico (70%)
Catkin		Jenny (40%)
Dijon	Zac (100%)	Calico (93%)
Doolittle	Zac & Wanda (50%)	
Mulberry	Zac (100%)	Laura (78%)

The Side B cats, Carbonel and Catkin, were brothers. Carbonel Followed and Approached Mulberry, Close-Sniffed (and Evaded) Catkin, Swiped and Rested with Dijon (and Evaded). Catkin Approached Mulberry, Evaded, Rubbed, Close Sniffed and Rested with Carbonel. Dijon and Doolittle were also brothers; Dijon Followed, Evaded and Rested with Carbonel, Approached Catkin (and Evaded him) and Mulberry (and Close Sniffed her). On the other hand, Doolittle Followed and Approached Mulberry, but Close Sniffed Carbonel and Catkin. The first pair of brothers interacted quite often, while the second two did so extremely rarely. The single Juvenile Female on Side B was Mulberry; she Followed and Rested with Carbonel, Approached Carbonel and Catkin (also Rubbing and Close Sniffing him), and Evaded Dijon and Doolittle. Relatively few amicable actions were seen from the B group, and were confined to Male-Female interactions, and to Resting coalitions.

4.3.6. KITTEN INTERACTIONS

When most behaviour was considered, Kittens Approached others at by far the greatest rate, and then Played Socially, Body Rubbed and Followed (Figure 4.7.a). Various other activities were performed much less often. Of all Adults and Juveniles, when the total rate of initiation by Kittens was considered (Figure 4.7.b), mothers received the highest levels; Poppy had the highest rate, followed by Daisy, Calico, Becky and Tessa. Obviously, littersize played little role, as the top-ranked Females had somewhat smaller litters. Jenny also had a lot of attention; she was seen suckling Kittens for weeks after the loss of her own litter in 1988. Wanda and Laura, despite helping most years (and despite the contributions from Wanda's own litters) were not major recipients. Zac, the Male in Group B, received far more Kitten attention than his counterpart in Group A, Trossachs, who seemed to actively avoid Kittens.

The relative proportions of behaviour were found for each Focal recipient. Becky was the subject of much Approach and Play, as were Tessa and Daisy; Bojangles was mainly Approached and Followed; Brigit was also Rubbed quite a lot. Calico was Approached, Rubbed and Followed; like Wanda, Carbonel was Approached and Evaded; Catkin was Approached and Rubbed, as was Dijon, while Doolittle received more Swipes and Tail Lashing than most other cats. Jenny was Approached and Rubbed, as was Katrina; Laura received little more than Approaches, as with Molly and Pippin. Rates to Mulberry and Pishi were low, and consisted mainly of Approaches, with some Following, Rubbing and Sniffing; Pansy was Approached and Sniffed. Poppy received twice as much of most activities, and was Approached, Followed and Groomed the most. As for the resident Males, Trossachs received Approaches, Evasion and Follows only, while Zac was Approached and Rubbed most.



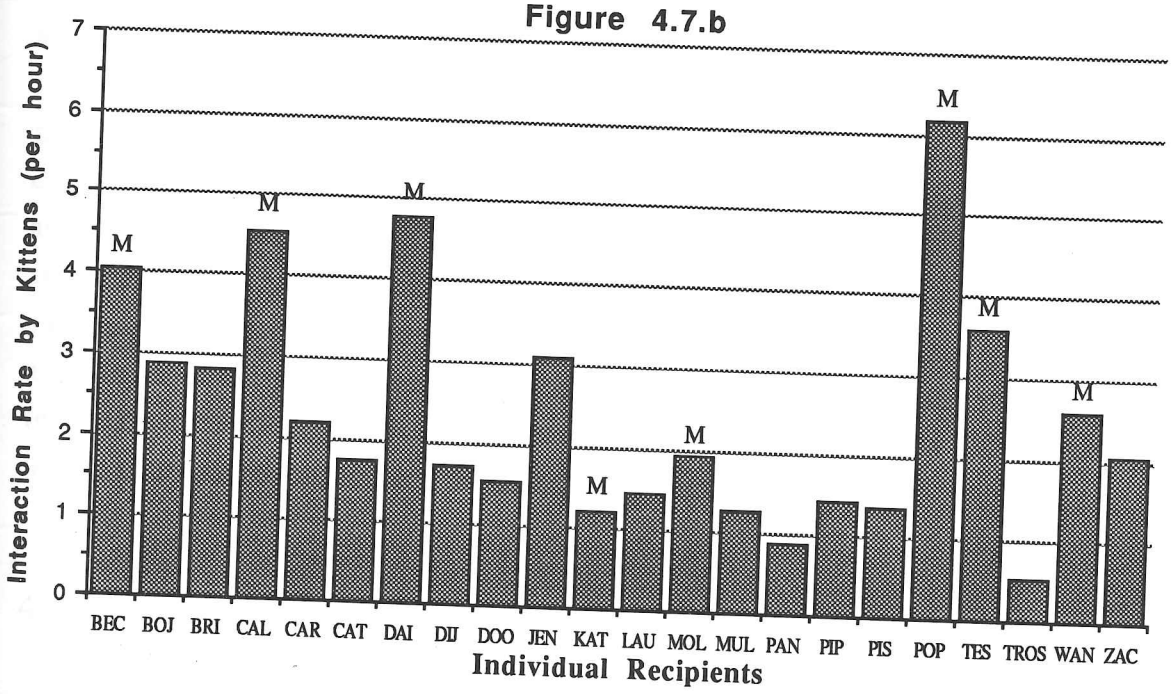


Figure 4.7: The rate of Kitten-initiated behaviour patterns. As Kittens were not Focal subjects, these values are from behaviour directed by Kittens to Focal individuals, and have been weighted by the availability of each recipient. (a) The rate over all possible recipients (weighted by the total observation time); (b) The sum of all initiations to each Focal individual (weighted by the observation time for each individual). Mothers are marked with "M".

In general, mothers were Rubbed and Played with a lot more than most other cats, and Approach rates to them were higher. Kittens definitely distinguished between individuals and responded differentially, probably in response to the actions of the older cats. Those individuals who received little behaviour from Kittens also initiated little (e.g. Trossachs, Pansy, Katrina, Zac and Laura), while cats who interacted with Kittens more contributed their own attentions too (e.g. Poppy, Calico, Becky, Tessa, Jenny and Molly). The details of these relationships are further expressed in Section 4.4.1.

Juveniles rarely Followed Kittens, except for the attention paid to Cleo by Dijon and Doolittle (who seemed to regard her as a viable Mounting object). Of the other Focal behaviour, there was little clear preference by Juveniles over different actions. Those seven Kittens who remained in 1989 were generally the biggest recipients, if only because of their greater availability.

4.3.7. DYAD SUMMARY

Dyads differed among themselves in the types and rates of behavioural activity observed. There were also dichotomies in the amounts of each behaviour pattern initiated and received within the dyad members. All cats seemed to have more common, or preferred partners for different actions, and with breeding Females, these often corresponded to cooperative partners and helpers (with affiliative behaviour patterns, among others). Overall, Males Followed and Approached their Female counterparts more, and appeared to have preferences for certain Female interaction recipients. Juvenile siblings showed variation in their activities together and with Adults. Kittens Approached and Played at the greatest rates with others, and mothers were their preferred partners (especially for Rubbing). Young Adult Males dispersed from the Group B after a period of intense agonistic encounters with the older Adult Male.

4.4. THE INDIVIDUAL

4.4.1. FEMALES

The eight most common Focal patterns were considered (not including the more problematic Rest/Sleep in Contact), and summed to obtain a hourly rate for each Female; significant individual differences became apparent for actions directed toward others ($H= 15.794$, $p<0.05$, $df= 8$, $n= 207$), but were less clear for those received from others ($H= 15.042$, $p=.059$, $df= 8$, $n= 53$). Jenny and Poppy initiated the greatest

numbers of actions to other cats, and, along with Tessa, also received the highest rate from other Adults.

Females in oestrus often act more erratically than usual (Dards 1979), spending a portion of their time running, cavorting and jumping into trees; there was also the occasional example of urine-spraying (n=3) and treading the ground with forepaws (n=4). Approximately equal numbers of tree-climbing cases were seen for the two groups (n=32,27), and most individuals engaged in this activity at some stage over the observation period. Only six of the eighteen Females were recorded as performing lordosis, and this included three Females who failed to breed during the study. Females also spent some time Rolling and receiving Rolls, as summarised in Figure 4.8.a.

Several of the Females were never observed to be mated but produced litters (e.g. Becky), while others were mated but failed to breed (e.g. Pansy, Brigit, Laura). It is likely that much more mating occurred than was recorded, if only because cats tend to undergo intensive bouts during oestrus (lasting a day or more, only a part of which was sampled).

Females varied in the amount of Ear Flattening that they exhibited, from 1 (Katrina) to 110 (Pansy), and 91% of these intervals had no recipient, with much of the remainder being directed toward Males. Tail Lashing was similar, and varied from 3 (Pansy) to 124 (Jenny), with 79% to no obvious recipient and most of the rest to Males. Only Females were seen to perform Piloerection (especially Tessa and Daisy); half the intervals had no recipient, 31% involved other Adult Females and 8% included Adult Males. Juvenile Males and Kittens received an additional 4% each, while one Juvenile Female accounted for the remaining 4%. Those Bites that were not directed by Males to Females in the course of mating were delivered by Females mainly to Male Juveniles and to Kittens. Adult Females were responsible for initiating 31% of all Fights, mainly with other Females; Poppy and Daisy were the main recipients of such agonism.

Object Play was predominantly performed by Adult Females, in particular Katrina and Wanda, who gave 52% of all counts; many Females were never seen engaged in this activity. Females contributed varying amounts of Nursing observations (Figures 4.8.b & c); surprisingly, the individual to perform the greatest amount was Jenny, the one Female who consistently abandoned her own litters but seemed amiable to allosuckling. Some Females tended only to their own litters while others were more open to advances from other Kittens.

Females showed individual differences in the amount of vocalisations they made; the only Calls were made by Molly, often to her Kittens; of the Yowls, all were made to Adult Males (n=11) or Kittens (n=6). Meows were used more generally, and were either made with no obvious recipient (n=33) or to Kittens (n=33), with the occasional Meow to Males (n=5) and other Females (n=1). Growls and Hisses were mainly made by

Figure 4.8.a

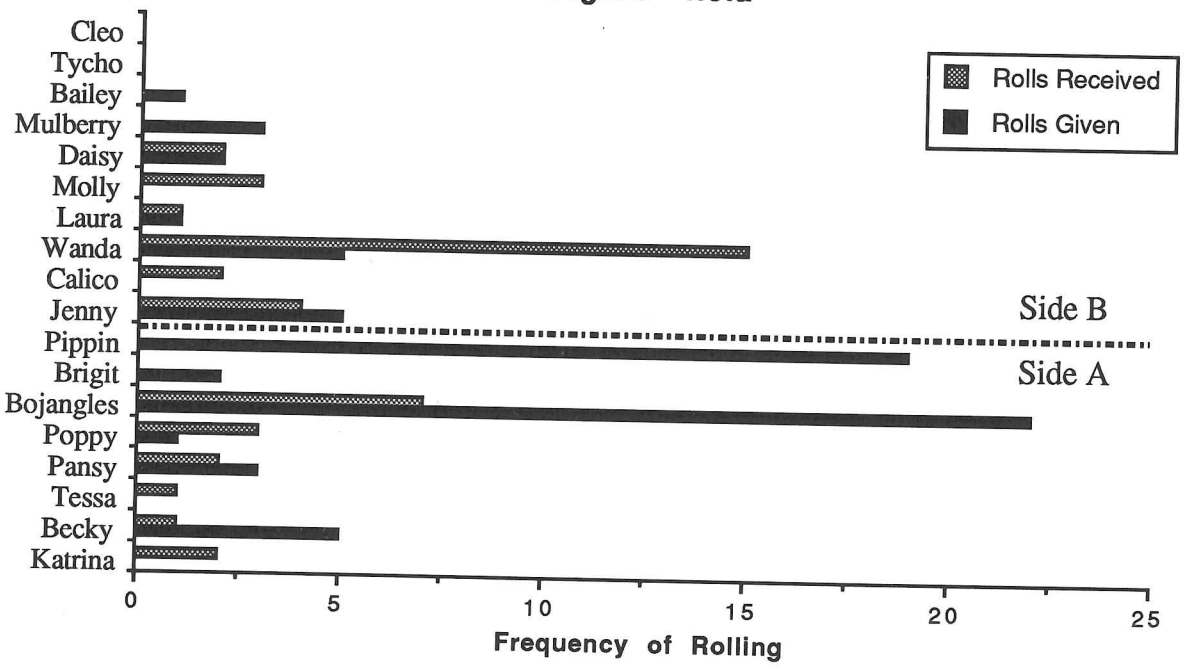


Figure 4.8.a: The frequency of Rolling initiated and received by each Female. The three cats at the top are Kittens (Tycho and Bailey from Group A and Cleo from Group B), and the remaining Juveniles and Adults are presented in their designated Groups. The measures are taken from Occasional data and represent actual frequency of occurrences.

Figure 4.8.b

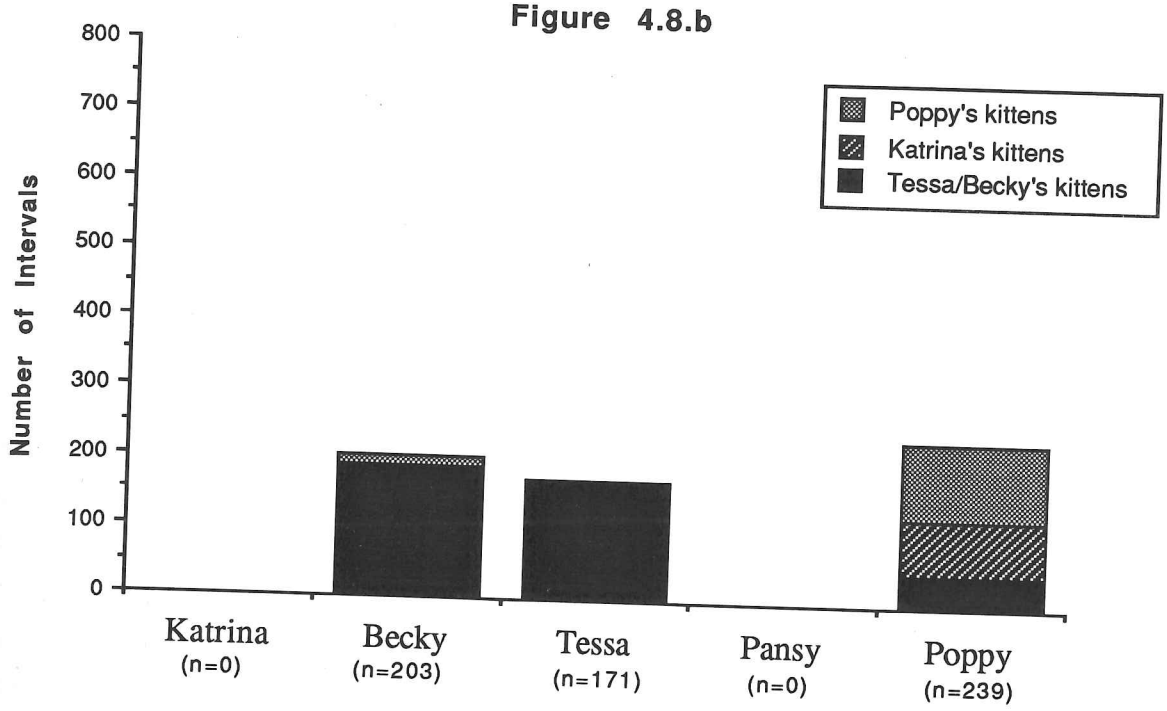


Figure 4.8.c

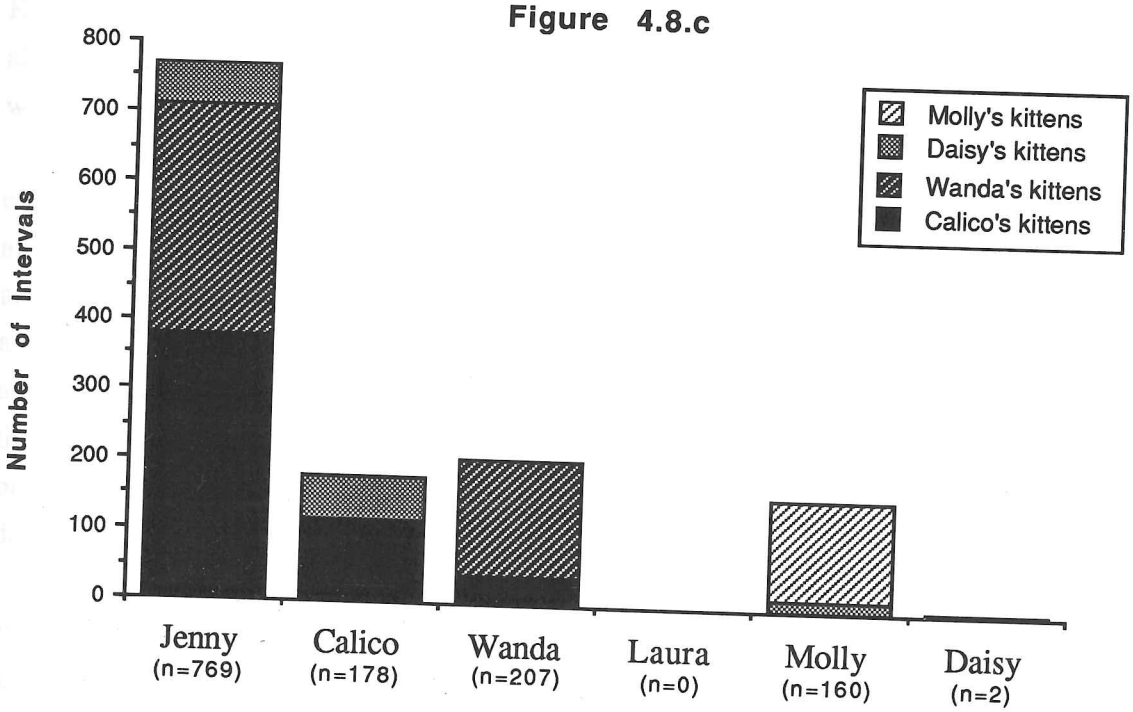


Figure 4.8: Nursing by Adult Females, and the distribution of kittens suckled. Both own kittens and other kittens are included. Values are presented as the number of Focal observation intervals in which a Female was seen suckling kittens. The sum total is given as "n" for each individual. (b) Group A; (c) Group B.

Females to Males (41%), Kittens (40%), and other Females (16%). Few Brrr and Purrs were heard from Females, and many of these had no recipient; a scant 8% of Brrr were to Males and 20% to Kittens; almost all Purrs were contributed by a single interaction in which Wanda Purred in the presence of Zac (97%). Scratching displayed little variation among individuals, although Laura did somewhat less (n=9) and Molly did the most (n=34).

Females were tested for differences in common behaviour directed toward Kittens, especially looking for contrasts between their relationships with their own and other litters. First, the various mothers were compared for each activity, but no significant differences were found (Table 4.8); however, Calico and Poppy had the highest ranks for level of interaction over many categories, such that Calico Followed, Approached, Body Rubbed, Close Sniffed and Rested more with Kittens, while Poppy Evaded, Body Rubbed, Close Sniffed and Groomed them. Tessa had the highest level of Swiping. There were seasonal differences, and these are explored in detail in Section 4.5. Only Calico differed in actions to Kittens, in that she Close Sniffed her own Kittens more ($U= 7$, $Z= -1.964$, $p<0.05$); Tessa was similar, in that she directed more actions to her own Kittens, but the difference was not significant ($U= 9$, $Z= -1.892$, $p= .059$); the analyses of all other Females were non-significant when activities toward own versus other Kittens were compared.

Individual Females varied considerably in the amount of retrieval behaviour exhibited. Retrieval was one pattern that was not initially included as a Focal activity, but appeared in Occasional observation recording. Retrieval is a characteristically maternal action in which a Female approaches a Kitten, either her own or that of another Female, and picks it up by the nape of the neck in her jaws. Most Kittens respond by going limp and allowing the Female to carry them for some distance; the ultimate destination is often the current nest occupied by the Kitten and/or the Female. Retrieval behaviour is probably one method by which a mother keeps her Kittens in one location and out of immediate danger.

Primiparous mothers generally showed no retrieval behaviour. The single exception was Wanda, who was the most avid conveyor of Kittens; Wanda was only seen to retrieve her own Kittens (once) or those of Calico (eighteen times), which she was attempting to allomother despite their advanced age. Of the experienced mothers, only Calico, Tessa and Poppy were observed to perform any retrievals; Calico's single action was to fetch Jenny's principally abandoned litter and bring them to Jenny, who then made a brief but ill-fated attempt to care for them. Tessa was seen to retrieve a Kitten once (her own), while Poppy performed six retrievals. Molly, Daisy, Katrina and Becky were never seen to retrieve a Kitten. Non-breeding Females (Laura and Pansy) showed 4 retrieval actions between them.

Table 4.8: Differences in Female Behaviour to Kittens, Using a Kruskal-Wallis Test. A significant result would indicate differences between breeding Females in the rates of behaviour initiated to Kittens.

Behaviour	**df**	**n**	**H**	**p**
Follow	8	77	12.290	.139
Approach	8	77	3.296	.915
Evade	8	77	4.443	.815
Body Rub	8	77	4.593	.800
Close Sniff	8	77	4.658	.794
Groom	8	77	7.783	.455
Swipe	8	77	12.328	.137
Rest in Contact	8	77	12.380	.135

4.4.2. MALES

Overall, the two founding Males acted as the net initiators for a number of less common actions, including Mounting, Copulation, Ear Flattening and Biting, while Zac also initiated the majority of Tail Lashes and Fights for Side B. Trossachs also initiated most of the Meow/Yowl/Call vocalisations for Side A. The two Males were net recipients of Meow/Yowl/Call and Growl/Hiss vocalisations, Ear Flattening, Tail Lashing and Rolling behaviour (Figure 4.9). When all the Mounting data were considered, all Males were seen to make at least one attempt, with the exception of those Males born in 1988 and 1989. In Side A, Trossachs performed 72% of all Mounts, with the remainder enacted by Pishi; on Side B, Zac had a number of attempts similar to those of Trossachs, but these only accounted for 41% of Mounts, with the rest by Dijon (24%), Carbonel (22%), Doolittle (12%) and Catkin (1%). No specific aggressive competition was seen between Males for access to Females, but the continual agonism between Zac and several of his sons was sparked when he came across the younger Males engaged in mating; never was a Male seen to Mount a Female after chasing away his predecessor, and many times, all Males were seen congregated around Females in oestrus, often with no agonistic incidences.

Despite the fact that all Males were seen to Mount other cats, only a few achieved successful copulation. These included Trossachs (n=23), Zac (n=15), Pishi (n=2), Doolittle (n=2) and Carbonel (n=1); Catkin and Dijon were never observed to reach intromission, although it is possible that they were more efficient in unsampled encounters.

Adult Males were seen to occasionally direct a Paw toward other cats (n=4), always Female. Males, as mentioned, performed the highest levels of Ear Flattening and Tail Lashing; most of the Ear Flattening (90%) was directed generally, and the rest mainly to other Males. In terms of Tail Lashing, Zac and Trossachs differed greatly, with Zac performing the greatest amount and Trossachs contributing one of the smallest levels; as with Ear Flattening, most was directed to no specific recipient, and the rest to other Males. A mere 10% involved Females, and these were often in the context of mating attempts. Only Zac was recorded as initiating Fights, and he accounted for 57% of the total; Trossachs was the recipient of some attention from Zac, but never initiated any Fights.

Males were the common contributors to general vocalisation; Trossachs Called while Zac did not; Yowls were frequent, and when directed at a specific other, were often to potential intruders (e.g. the corresponding Male in the other group, and a passing feral Female). Males tended to Meow less than Females (6% of the total), and nearly half of these were directed to each other. While Males received much of the Hisses and Growls, they only initiated 6%, and these were more or less equally distributed to other

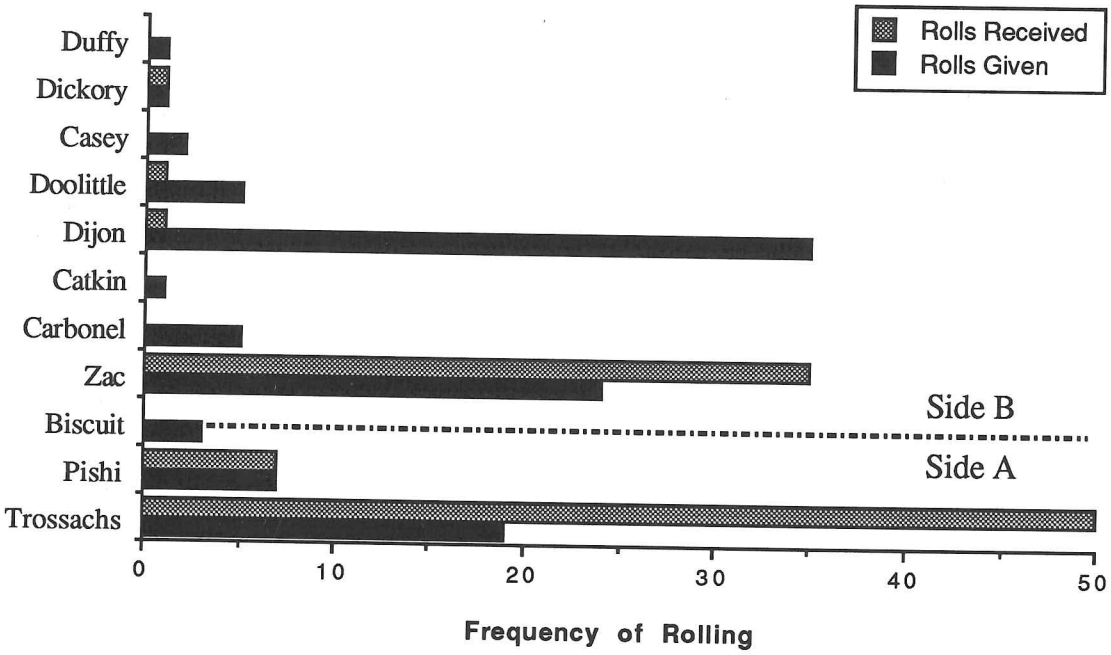


Figure 4.9: The frequency of Rolling initiated and received by each Male. Adults, Juveniles and Kittens are included for each Group. The measures are taken from Occasional data and represent actual frequency of occurrences.

Males and Females. Males performed 52% of all Brrr sounds (all by Zac), half to no particular cat and the other half to Adult Females; Males were not heard to Purr.

Scratching varied somewhat between the two Adult Males, such that Trossachs performed about twice as much as Zac; however, there was a general spread of values when additional Males were examined, and both Adults fell within this range.

4.4.3. JUVENILES

The rates of common behaviour patterns varied with each individual Juvenile, and the overall statistics were presented in Figure 4.5.c. The distribution of behaviour rates for each individual is shown in Table 4.9. When Rest in Contact was excluded, being several orders of magnitude larger than other rates, differences were apparent. Approach rates were consistently higher, then Follow rates. Bojangles, Brigit and Pippin performed more affiliative actions, including Body Rub, Groom and Close Sniff; Mulberry was similar, except for a raised Evade rate. All the Males, however, showed higher rates of Evade as well as Close Sniff, and had much lower levels for Rub and Groom.

Rare behaviour showed varying patterns. Young Females were the net recipients of Mounting attempts in both groups (e.g. Bojangles and Cleo). When all counts of Mounting were considered, including those from "Occasional Observation", young Males were also seen to receive a number of Mount attempts (n=17), although they initiated a few more (n=25), mainly to Kittens. Juveniles engaged in a few Pawing encounters, both as initiators (n=22) and recipients (n=19); most of these included Females (88%). Juvenile Males were major recipients of Fights from Adult Males (i.e. Zac), amounting to 59% of Male initiations, as well as 26% of Female initiations. Juvenile Females were almost never recipients of escalated agonism, and only from Adult Females (n=2).

Juveniles performed 48% of all Object Play, particularly the Males of Side B (36%). Very few vocalisations were recorded for Juveniles: all Calls were made after the individuals became Adult (n=9); the sparse number of Yowls were made mainly to Males (n=4 of a total of 6); and most Meows were made without a particular recipient being observed (71%). All but one Hiss/Growl were made to Males, and there was a single general Brrr voiced by a Juvenile Female. The louder and more obvious sounds were occasionally made by Juveniles, but they were less evident than in Adults, and quieter noises were probably incompletely sampled.

Table 4.9: Behaviour Rates (per hour) for All Focal Juveniles

Name	Follow	Approach	Evade	C/H/R	B/Rub
Bojangles	.312	.342	.033	.003	.046
Brigit	.275	.441	.066	0	.073
Pippin	.239	.345	.043	.010	.086
Pishi	.192	.295	.043	0	.007
Carbonel	.192	.536	.104	.066	.139
Catkin	.022	.085	.016	.003	.006
Dijon	.243	.480	.085	0	.003
Doolittle	.050	.133	.057	0	0
Mulberry	.025	.237	.114	.003	.044

	Close Sniff	Rest in Contact	Groom	Swipe
Bojangles	.050	49.331	.063	.033
Brigit	.090	7.154	.003	.017
Pippin	.056	13.714	.013	.010
Pishi	.053	10.239	0	.003
Carbonel	.091	42.282	.003	.009
Catkin	.016	62.587	.019	0
Dijon	.104	12.425	.019	.019
Doolittle	.025	0	.006	.009
Mulberry	.038	14.211	.066	.003

4.4.4. KITTENS

Kittens received a number of Mount attempts, both from Adult Males (n=3) and Juvenile Males (n=19); only Juveniles Mounted Male Kittens, but all older Males directed their attentions to a few very young Kittens, from only a few months old. These examples occurred when there were Adult Females present and being Mounted around the same time; it is possible that the focus by Juveniles on these small Kittens incited the Adult Male (i.e. Zac) to act similarly. Intromission was not seen for these attempts.

Of a total of 98 Pawings, 17% were given by Adults to Kittens, 4% by Juveniles to Kittens, 2% by Kittens to Juveniles, and 23% by Kittens to Adults. Relatively few of the Paws involving Kittens were with the mother (33%), but most were with an older Female of some description.

Kittens were never involved in severe Fights, and they were infrequently the objects of less intense agonism, such as Ear Flattening, Tail Lashing and Biting. Kittens were the main contributors to the recordings of Social Play, but only those interactions with non-Kittens were included in the Focal data. It is likely that huge amounts of both Object and Social Play occurred without being recorded, and it is not possible to describe the details of Play between Kittens. Kittens primarily Played with Adult Females, including their mothers, allomothers and non-breeding helpers.

4.4.5. INDIVIDUAL SUMMARY

Individual variation was seen in the rates of performance of all activities. Females varied in the proportion of Nursing they did with their own versus other Kittens, and there were some overall differences between the two groups in the Nursing patterns. Retrieval of Kittens also differed for individual Females. Overall, Males were the net initiators for many of the less common activities. No specific aggressive competition was seen between Males for access to Females and Males were never seen to Mount a Female after chasing away a predecessor. Multiple Males were seen congregated around Females in oestrus, often with no serious agonistic interactions. All Males were seen to make Mount attempts, but not all of the individual Males copulated successfully.

4.5. SEASONALITY

4.5.1. METHODS

Seasons were defined as in Chapter 3 (Section 3.5.1) such that the year was divided by reproductive state into Gestation, Breeding and Winter (non-oestrus) periods. The few weeks which did not fit into these stages were not included toward a final behaviour rate, to keep the measures as consistent as possible across individuals. The data from each Female which reproduced were divided into her respective season periods, and the rates of all behaviour directed to her, and by her, were considered for each of those intervals. Analyses on these seasonal data included Spearman Correlation, Kruskal-Wallis and Mann-Whitney U-tests, as the predominant rates were zero for many potential dyads (thus precluding parametric tests). Monthly behaviour rates were also calculated, both as a means of comparison with other studies, and to examine more closely the role of weather and the validity of partitioning the data into seasons. The results of weather correlations are presented first, followed by monthly scores and then "seasonal" values.

4.5.2. RESULTS

The first form of comparison dealt with monthly Focal behaviour rates. These were calculated for the nine main behaviour patterns, based on initiations by Adults to other Adults and Juveniles, as these were the individuals present throughout the entire study. Monthly rates were correlated against various weather measures, both over all Adults and each group. Following decreased as Temperatures increased for both groups (All: r_S= -.772, Z= -2.784, $p<0.01$; Side A: r_S= -.728, Z= -2.626, $p<0.01$; Side B: r_S= -.581, Z= -2.094, $p<0.05$; all n= 14, also for Minimum Temperature); AlloGrooming increased as Temperatures (and Sun hours) increased for Group B (Maximum Temperature: r_S= .881, Z= 3.177, $p<0.01$; Minimum Temperature: r_S= .858, Z= 3.094, $p<0.01$; Sun: r_S= .625, Z= 2.253, $p<0.05$), as did Close Sniffing (Maximum Temperature: r_S= .64, Z= 2.309, $p<0.05$; Minimum Temperature: r_S= .569, Z= 2.052, $p<0.05$; Sun: r_S= .609, Z= 2.195, $p<0.05$). Also, increased rainfall was associated with increases in Cheek/Head Rub rate in Group B (r_S= .578, Z= 2.083, $p<0.05$). The maximum rate for most patterns occurred in February (Side A) and January to May (Side B), although this varied with the type of activity.

The two cat groups were then tested for associations in monthly rates of behaviour (Table 4.10.a). Barring the more pro-social aspects of Rubbing, Grooming and Resting in Contact, these monthly rates were related, which again indicates the more

general tenor of those actions (versus the more individualistic contact activities). Monthly rates were examined for associations between them, and a few correlations were found (Table 4.10.b), such that months with lots of Following tended to have more Body Rubbing but less Grooming; high Approach rates also saw high rates of Evading, Rubbing and Sniffing, which were in turn inter-related, while Sniffing and Swiping were also associated. The groups showed a few differences, based on the lack of synchrony in amicable behaviour. These results point strongly to seasonal changes in behavioural repertoire, responding to the dynamics of mating and breeding, such that investigative actions are rife in the mating times, and certain activities occur in clusters (whether in the winter, gestation or breeding). The next consideration uses the concept of reproductive seasons to examine these suggestions more closely.

The behavioural rates for analysis of seasons were first examined to see if the rates calculated over the "reproductive year" (and not over all the recorded Focal data) showed the same trends as in the previous sections. When the total hourly rates (over the whole "reproductive year") of the nine main behavioural actions were examined for correlations, across all dyads (n=301), most combinations of Focal actions were significantly linearly related, with the exception of Evade and Groom, Cheek/Head Rub and Groom, Body Rub with Groom and Swipe, and Groom with Swipe (Table 4.10.c). The pattern of associations varied little whether directed to or by the Focal Females. When the behaviour to others was compared, breeding Females showed significant differences for Grooming (Jenny and Poppy ranked highest), Swiping (Wanda, then Jenny) and Resting in Contact (Jenny and Calico); as for the recipients of such behaviour, Approach (Zac, Laura and Bojangles), Evade (Zac, Trossachs and Carbonel) and Groom (Biscuit, Carbonel, Duffy, Casey and Cleo) were significantly different (Table 4.10.d). When the recipients are classed by age group, into Adult, Juvenile and Kitten, large differences are seen for all behaviour but Resting in Contact (Table 4.10.e); Kittens received the most attention (except for Approach, more of which went to Adults), followed by Adults and then Juveniles. When the sex of the recipient was considered, the Females Approached and Swiped Males more (Table 4.10.f).

A similar analysis was performed on actions to breeding Females over the reproductive year. Follow, Approach, Evade, Close Sniff, Groom and Rest in Contact all showed significant differences in the rates toward Females; Trossachs was the greatest initiator, except for Groom (by Poppy) and Resting (by Katrina). Of the Focal Female recipients, the only significantly different behaviour was Swiping, wherein Wanda and Bojangles were the highest-ranking receivers, followed by Poppy and Jenny. These results are summarised in Table 4.10.g. When the sex of initiators to Females was

Table 4.10.a: Correlations Between Monthly Rates in Two Groups (n=14). A significant probability level means that there is a linear relationship between the ranks of the monthly rates of behaviour for Group A versus Group B.

Behaviour	r_s	**Z**	**p**
Follow	.679	2.449	<0.05 *
Approach	.727	2.623	<0.01 **
Evade	.578	2.084	<0.05 *
Cheek/Head Rub	.027	.098	.922
Body Rub	.183	.661	.509
Close Sniff	.582	2.100	<0.05 *
Groom	.120	.432	.666
Swipe	.554	1.999	<0.05 *
Rest in Contact	.400	1.442	.149

Table 4.10.b: Spearman Correlations Between Monthly Behaviour Rates (n=14). A significant result indicates that the ranks of the two behaviour rates (over all months) are linearly related. For example, months with high Follow rates (ranks) tend to have high Body Rub rates (ranks). Note that, due to the large number of variables tested together, significance levels should be taken as indicative and not absolute.

Behaviour 1	**Behaviour 2**	r_s	**Z**	**p**	
Follow	Approach	.385	1.387	.166	
Follow	Evade	.345	1.244	.214	
Follow	Cheek/Head Rub	. 427	1.539	.123	
Follow	Body Rub	.560	2.021	<0.05	*
Follow	Close Sniff	.174	.626	.531	
Follow	Groom	-.759	-2.737	<0.01	**
Follow	Swipe	-.015	- .055	.956	
Follow	Rest in Contact	-.121	- .436	.663	
Approach	Evade	.780	2.813	<0.01	**
Approach	Cheek/Head Rub	.605	2.182	<0.05	*
Approach	Body Rub	.670	2.417	<0.05	*
Approach	Close Sniff	.710	2.560	<0.05	*
Approach	Groom	-.315	-1.134	.257	
Approach	Swipe	.415	1.498	.134	
Approach	Rest in Contact	-.248	- .895	.371	
Evade	Cheek/Head Rub	.620	2.237	<0.05	*
Evade	Body Rub	.578	2.084	<0.05	*
Evade	Close Sniff	.613	2.211	<0.05	*
Evade	Groom	-.315	-1.134	.257	
Evade	Swipe	.270	.975	.330	
Evade	Rest in Contact	-.095	- .341	.733	
Cheek/Head Rub	Body Rub	.847	3.054	<0.01	**
Cheek/Head Rub	Close Sniff	.741	2.673	<0.01	**
Cheek/Head Rub	Groom	-.240	- .866	.387	
Cheek/Head Rub	Swipe	.268	.968	.333	
Cheek/Head Rub	Rest in Contact	-.042	- .151	.880	
Body Rub	Close Sniff	.560	2.021	<0.05	*
Body Rub	Groom	-.482	-1.737	.082	
Body Rub	Swipe	.209	.753	.452	
Body Rub	Rest in Contact	-.182	- .658	.511	
Close Sniff	Groom	.143	.516	.606	
Close Sniff	Swipe	.560	2.021	<0.05	*
Close Sniff	Rest in Contact	.187	.674	.501	
Groom	Swipe	.158	.571	.568	
Groom	Rest in Contact	.460	1.658	.097	
Swipe	Rest in Contact	-.011	- .040	.968	

Table 4.10.c: Overall Behaviour Rates over the Reproductive Year (n=301). Tests were first performed over all dyads (column labelled "p"), and then for rates initiated by breeding Females to other cats ("To others") and other cats to breeding Females ("By others"). A significant result means that the ranks of the two behaviour rates are linearly related, such that, for example, a dyad with a high (ranked) rate of Following will tend to show a high (ranked) rate of Approaching. Note that, due to the large number of variables tested together, significance levels should be taken as indicative and not absolute.

Behaviour	r_s	Z	p	To others	By others
Foll-Appr	.547	9.470	<0.001	***	***
Foll-Evade	.240	4.162	<0.001	**	**
Foll-C/H/R	.278	4.818	<0.001	***	p=.059
Foll-B/Rub	.270	4.674	<0.001	***	p=.100
Foll-C/Snf	.367	6.356	<0.001	***	***
Foll-Groom	-.130	-2.246	<0.05	p=.158	p=.580
Foll-Swipe	.315	5.456	<0.001	***	***
Foll-Rest/C	.127	2.192	<0.05	*	p=.318
Appr-Evade	.391	6.780	<0.001	***	***
Appr-C/H/R	.359	6.216	<0.001	***	***
Appr-B/Rub	.394	6.825	<0.001	***	**
Appr-C/Snf	.494	8.552	<0.001	***	***
Appr-Groom	-.114	-1.974	<0.05	*	**
Appr-Swipe	.319	5.522	<0.001	***	***
Appr-Rest/C	.401	6.937	<0.001	***	***
Evade-C/H/R	.139	2.415	<0.05	**	p=.614
Evade-B/Rub	.239	4.135	<0.001	***	p=.350
Evade-C/Snf	.296	5.131	<0.001	***	**
Evade-Groom	.019	.333	.739	p=.663	p=.674
Evade-Swipe	.274	4.747	<0.001	***	**
Evade-Rest/C	.235	4.066	<0.001	***	*
C/H/R-B/Rub	.450	7.794	<0.001	***	***
C/H/R-C/Snf	.380	6.582	<0.001	***	***
C/H/R-Groom	.065	1.122	.262	p=.973	**
C/H/R-Swipe	.235	4.067	<0.001	***	p=.120
C/H/R-Rest/C	.195	3.375	<0.001	*	*
B/Rub-C/Snf	.324	5.609	<0.001	***	*
B/Rub-Groom	.072	1.246	.213	p=.448	p=.063
B/Rub-Swipe	.051	.879	.379	p=.135	p=.563
B/Rub-Rest/C	.231	4.007	<0.001	***	*
C/Snf-Groom	.276	4.788	<0.001	***	***
C/Snf-Swipe	.289	5.005	<0.001	***	***
C/Snf-Rest/C	.349	6.038	<0.001	***	***
Groom-Swipe	-.031	- .535	.593	p=.419	p=.609
Groom-Rest/C	.388	6.712	<0.001	***	***
Swipe-Rest/C	.202	3.503	<0.001	*	**

Table 4.10.d: Behaviour by Females to Others over the Reproductive Year, Using a Kruskal-Wallis Test. A significant result indicates differences among breeding Females in the rates of initiated behaviour (or among other cats as the recipients of behaviour initiated by those breeding Females).

Behaviour	**df**	**n**	**H**	**p**
INITIATORS (Females)				
Follow	8	207	15.365	.052
Approach	8	207	4.650	.794
Evade	8	207	13.880	.085
Cheek/Head Rub	8	207	2.523	.961
Body Rub	8	207	3.901	.866
Close Sniff	8	207	10.305	.244
Groom	8	207	23.760	<0.01 **
Swipe	8	207	27.488	<0.001 ***
Rest in Contact	8	207	33.009	<0.001 ***
RECIPIENTS (All Others)				
Follow	63	180	69.148	.278
Approach	63	180	137.425	<0.001 ***
Evade	63	180	93.695	<0.01 **
Cheek/Head Rub	63	180	48.898	.904
Body Rub	63	180	60.168	.578
Close Sniff	63	180	66.099	.370
Groom	63	180	85.738	<0.05 *
Swipe	63	180	75.020	.143
Rest in Contact	63	180	65.948	.375

Table 4.10.e: Behaviour by Females to Different Age Classes over the Reproductive Year, Using a Kruskal-Wallis Test. A significant result means that the rates of behaviour (ranked) differ with the age class of the recipient. For example, breeding Females Follow Kittens more than Adults or Juveniles.

Behaviour	**df**	**n**	**H**	**p**		
Follow	2	207	39.619	<0.001	***	(K>A>J)
Approach	2	207	119.920	<0.001	***	(A>K>J)
Evade	2	207	23.412	<0.001	***	(K>A>J)
Cheek/Head Rub	2	207	16.867	<0.001	***	(K>A>J)
Body Rub	2	207	19.528	<0.001	***	(K>A>J)
Close Sniff	2	207	6.301	<0.05	*	(K>A>J)
Groom	2	207	41.117	<0.001	***	(K>>A=J)
Swipe	2	207	10.926	<0.01	**	(K>A>J)
Rest in Contact	2	207	.711	.701		(K>A>J)

Table 4.10.e: Behaviour by Females to Different Age Classes over the Reproductive Year, Using a Kruskal-Wallis Test. A significant result means that the rates of behaviour (ranked) differ with the age class of the recipient. For example, breeding Females Follow Kittens more than Adults or Juveniles.

Behaviour	**df**	**n**	**H**	**p**		
Follow	2	207	39.619	<0.001	***	(K>A>J)
Approach	2	207	119.920	<0.001	***	(A>K>J)
Evade	2	207	23.412	<0.001	***	(K>A>J)
Cheek/Head Rub	2	207	16.867	<0.001	***	(K>A>J)
Body Rub	2	207	19.528	<0.001	***	(K>A>J)
Close Sniff	2	207	6.301	<0.05	*	(K>A>J)
Groom	2	207	41.117	<0.001	***	(K>>A=J)
Swipe	2	207	10.926	<0.01	**	(K>A>J)
Rest in Contact	2	207	.711	.701		(K>A>J)

Table 4.10.f: Behaviour by Females to Different Sex Classes over the Reproductive Year, Using a Mann-Whitney U-test. For example, breeding Females Approach other Females at higher (ranked) rates than they Approach Males.

Behaviour	**n (m,f)**	**U**	**Z**	**p**		
Follow	81,110	4219	- .937	.349		
Approach	81,110	3565.5	-2.480	<0.05	*	(F>M)
Evade	81,110	4282	- .498	.619		
Cheek/Head Rub	81,110	4450	- .031	.975		
Body Rub	81,110	4204	-1.081	.280		
Close Sniff	81,110	4230	- .646	.519		
Groom	81,110	4169.5	- .826	.409		
Swipe	81,110	3655.5	-2.666	<0.01	**	(M>F)
Rest in Contact	81,110	4240.5	- .586	.558		

Table 4.10.g: Behaviour to Females over the Reproductive Year, Using a Kruskal-Wallis Test. This table is the same as Table 4.10.d, using behaviour rates initiated to breeding Females (rather than rates initiated by those Females).

Behaviour	**df**	**n**	**H**	**p**
INITIATORS				
Follow	18	94	43.118	<0.001 ***
Approach	18	94	46.329	<0.001 ***
Evade	18	94	33.546	<0.05 *
Cheek/Head Rub	18	94	9.471	.948
Body Rub	18	94	18.590	.418
Close Sniff	18	94	42.694	<0.001 ***
Groom	18	94	34.295	<0.05 *
Swipe	18	94	22.055	.230
Rest in Contact	18	94	46.391	<0.001 ***
RECIPIENTS (Females)				
Follow	13	94	15.351	.286
Approach	13	94	19.901	.098
Evade	13	94	17.800	.165
Cheek/Head Rub	13	94	14.007	.373
Body Rub	13	94	12.418	.494
Close Sniff	13	94	11.222	.592
Groom	13	94	12.988	.449
Swipe	13	94	23.136	<0.05 *
Rest in Contact	13	94	17.060	.197

Table 4.10.h: Behaviour to Females from the Different Sex Classes over the Reproductive Year, Using a Mann-Whitney U-test. As Table 4.10.f, with behaviour rates initiated towards breeding Females instead of rates initiated by those Females.

Behaviour	**n (m,f)**	**U**	**Z**	**p**		
Follow	21,73	394.5	-3.892	<0.001	***	(M>F)
Approach	21,73	644.5	-1.108	.268		
Evade	21,73	727	- .382	.703		
Cheek/Head Rub	21,73	766	- .009	.993		
Body Rub	21,73	577.5	-2.499	<0.05	*	(F>M)
Close Sniff	21,73	612.5	-1.470	.141		
Groom	21,73	634	-1.547	.122		
Swipe	21,73	630.5	-1.509	.131		
Rest in Contact	21,73	557	-1.973	<0.05	*	(F>M)

Table 4.10.i: Correlations Between Seasons for Focal Behaviour. As for preceding Tables 3.5.e and 4.10.c. Again, careful interpretation of significance levels is required with so many correlations.

	Females to Others				Others to Females			
Seasons	**n**	**r_s**	**Z**	**p**	**n**	**r_s**	**Z**	**p**
FOLLOW								
G1-B1	207	.150	2.148	<0.05	62	.281	2.193	<0.05
G1-G2	100	-.021	- .204	.838	28	.720	3.742	<0.001
G1-B2	50	.685	4.796	<0.001	15	.696	2.606	<0.01
G1-W	207	.235	3.375	<0.001	62	.370	2.893	<0.01
G1-G1'	171	.096	1.251	.211	50	.401	2.808	<0.01
G1-B1'	23	1	4.690	<0.001	8	.708	1.874	.061
B1-G2	100	.272	2.708	<0.01	28	-.113	- .586	.558
B1-B2	50	-.042	- .292	.771	15	-.232	- .87	.385
B1-W	207	.365	5.234	<0.001	62	.392	3.065	<0.01
B1-G1'	171	.263	3.435	<0.001	50	.250	1.750	.080
B1-B1'	23	.938	4.397	<0.001	8	.959	2.538	<0.05
G2-B2	50	-.029	- .204	.838	15	-.159	- .594	.553
G2-W	100	.295	2.937	<0.01	28	.459	2.384	<0.05
G2-G1'	100	.130	1.294	.196	28	.108	.564	.573
G2-B1'	23	1	4.690	<0.001	8	.708	1.874	.061
B2-W	50	.225	1.576	.115	15	.584	2.185	<0.05
B2-G1'	50	-.075	- .526	.599	15	.653	2.443	<0.05
B2-B1'								
W-G1'	171	.444	5.784	<0.001	84	.549	5.004	<0.001
W-B1'	23	.880	4.130	<0.001	8	-.216	- .571	.568
G1'-B1'	23	.938	4.397	<0.001	8	.581	1.538	.124
APPROACH								
G1-B1	207	.416	5.972	<0.001	62	.226	1.761	.078
G1-G2	100	.336	3.340	<0.001	28	.439	2.284	<0.05
G1-B2	50	.526	3.685	<0.001	15	.423	1.581	.114
G1-W	207	.429	6.163	<0.001	62	.613	4.786	<0.001
G1-G1'	171	.361	4.710	<0.001	50	.428	2.994	<0.01
G1-B1'	23	-.083	- .387	.699	8	.708	1.874	.061
B1-G2	100	.336	3.346	<0.001	28	.431	2.237	<0.05
B1-B2	50	.395	2.764	<0.01	15	.406	1.520	.129
B1-W	207	.474	6.800	<0.001	62	.321	2.510	<0.05
B1-G1'	171	.548	7.145	<0.001	50	.523	3.658	<0.001
B1-B1'	23	.076	.354	.723	8	.455	1.203	.229
G2-B2	50	.408	2.855	<0.01	15	-.013	- .048	.962
G2-W	100	.580	5.769	<0.001	28	.568	2.950	<0.01
G2-G1'	100	.517	5.149	<0.001	28	.613	3.184	<0.01
G2-B1'	23	.135	.632	.527	8	.156	.412	.680
B2-W	50	.081	.569	.570	15	.146	.546	.585
B2-G1'	50	.317	2.216	<0.05	15	.433	1.620	.105
B2-B1'								
W-G1'	171	.523	6.820	<0.001	84	.439	4.001	<0.001
W-B1'	23	.023	.107	.915	8	.450	1.191	.234
G1'-B1'	23	.265	1.245	.213	8	.655	1.732	.083

	Females to Others				Others to Females			
Seasons	**n**	**r_s**	**Z**	**p**	**n**	**r_s**	**Z**	**p**
EVADE								
G1-B1	207	.224	3.217	<0.01	62	.173	1.354	.176
G1-G2	100	-.076	- .759	.448	28	.036	.186	.852
G1-B2	50	.172	1.205	.228	15	-.133	- .496	.620
G1-W	207	.143	2.057	<0.05	62	.003	.025	.980
G1-G1'	171	.214	2.790	<0.01	50	.178	1.248	.212
G1-B1'	23	1	4.690	<0.001	8	1	2.646	<0.01
B1-G2	100	.106	1.058	.290	28	.038	.196	.845
B1-B2	50	.239	1.676	.094	15	-.184	- .689	.491
B1-W	207	.110	1.574	.116	62	.202	1.576	.115
B1-G1'	171	.206	2.684	<0.01	50	.555	3.883	<0.001
B1-B1'	23	.829	3.886	<0.001	8	.619	1.638	.102
G2-B2	50	-.084	- .588	.556	15	-.105	- .391	.696
G2-W	100	-.111	-1.109	.268	28	.141	.731	.465
G2-G1'	100	.007	.075	.941	28	.212	1.103	.270
G2-B1'	23	.782	3.667	<0.001	8	.565	1.496	.135
B2-W	50	.246	1.721	.085	15	-.133	- .496	.620
B2-G1'	50	.350	2.449	<0.05	15	-.133	- .496	.620
B2-B1'								
W-G1'	171	.194	2.529	<0.05	84	.189	1.724	.085
W-B1'	23	.740	3.469	<0.001	8	.560	1.480	.139
G1'-B1'	23	.829	3.886	<0.001	8	.833	2.205	<0.05
BODY RUB								
G1-B1	207	.218	3.129	<0.01	62	.150	1.173	.241
G1-G2	100	.342	3.407	<0.001	28	.720	3.742	<0.001
G1-B2	50	.971	6.794	<0.001	15	.627	2.347	<0.05
G1-W	207	.353	5.062	<0.001	62	.564	4.404	<0.001
G1-G1'	171	.569	7.423	<0.001	50	.746	5.224	<0.001
G1-B1'	23	.938	4.397	<0.001	8	1	2.646	<0.01
B1-G2	100	.335	3.335	<0.001	28	-.037	- .192	.847
B1-B2	50	.971	6.794	<0.001	15	-.105	- .391	.696
B1-W	207	.193	2.764	<0.01	62	.268	2.091	<0.05
B1-G1'	171	.317	4.137	<0.001	50	.128	.899	.369
B1-B1'	23	-.045	- .213	.831	8	1	2.646	<0.01
G2-B2	50	.942	6.596	<0.001	15	.825	3.087	<0.01
G2-W	100	.263	2.621	<0.01	28	.373	1.940	.052
G2-G1'	100	.431	4.287	<0.001	28	.489	2.542	<0.05
G2-B1'	23	.938	4.397	<0.001	8	1	2.646	<0.01
B2-W	50	.864	6.051	<0.001	15	.705	2.638	<0.01
B2-G1'	50	.915	6.407	<0.001	15	1	3.742	<0.001
B2-B1'								
W-G1'	171	.525	6.849	<0.001	84	.574	5.232	<0.001
W-B1'	23	-.066	- .308	.758	8	.708	1.874	.061
G1'-B1'	23	-.045	- .213	.831	8	.833	2.205	<0.05

	Females to Others				Others to Females			
Seasons	**n**	**r_s**	**Z**	**p**	**n**	**r_s**	**Z**	**p**
CLOSE SNIFF								
G1-B1	207	.194	2.791	<0.01	62	.283	2.210	<0.05
G1-G2	100	.239	2.381	<0.05	28	.293	1.521	.128
G1-B2	50	.044	.305	.760	15	-.409	-1.532	.126
G1-W	207	.261	3.746	<0.001	62	.444	3.467	<0.001
G1-G1'	171	.218	2.846	<0.01	50	.260	1.822	.068
G1-B1'	23	.880	4.130	<0.001	8	.833	2.205	<0.05
B1-G2	100	.166	1.652	.099	28	.026	.138	.891
B1-B2	50	-.160	-1.122	.262	15	-.098	- .368	.713
B1-W	207	.161	2.315	<0.05	62	.438	3.420	<0.001
B1-G1'	171	.166	2.169	<0.05	50	.287	2.010	<0.05
B1-B1'	23	.599	2.811	<0.01	8	.472	1.250	.211
G2-B2	50	-.049	- .345	.730	15	-.270	-1.009	.313
G2-W	100	.235	2.337	<0.05	28	.617	3.206	<0.01
G2-G1'	100	.182	1.807	.071	28	.154	.803	.422
G2-B1'	23	-.066	- .308	.758	8	-.283	- .750	.453
B2-W	50	-.049	- .345	.730	15	0	0	1
B2-G1'	50	.037	.258	.797	15	0	0	1
B2-B1'								
W-G1'	171	.324	4.220	<0.001	84	.348	3.170	<0.01
W-B1'	23	.647	3.033	<0.01	8	.425	1.125	.261
G1'-B1'	23	.663	3.112	<0.01	8	.592	1.565	.118
GROOM								
G1-B1	207	-.087	-1.242	.214	62	.953	7.444	<0.001
G1-G2	100	-.028	- .274	.784	28	.720	3.742	<0.001
G1-B2	50	-.048	- .333	.739	15	.906	3.391	<0.001
G1-W	207	.004	.052	.959	62	.187	1.461	.144
G1-G1'	171	.245	3.201	<0.01	50	-.036	- .253	.801
G1-B1'	23	.938	4.397	<0.001	8	1	2.646	<0.01
B1-G2	100	.120	1.196	.232	28	.900	4.678	<0.001
B1-B2	50	-.095	- .663	.508	15	1	3.742	<0.001
B1-W	207	-.058	- .835	.404	62	.778	6.078	<0.001
B1-G1'	171	-.081	-1.052	.293	50	.915	6.407	<0.001
B1-B1'	23	-.045	- .213	.831	8	1	2.646	<0.01
G2-B2	50	-.084	- .588	.556	15	.906	3.391	<0.001
G2-W	100	-.093	- .924	.355	28	.218	1.134	.257
G2-G1'	100	-.086	- .856	.392	28	-.077	- .399	.690
G2-B1'	23	-.066	- .309	.758	8	.833	2.205	<0.05
B2-W	50	-.144	-1.011	.312	15	.906	3.391	<0.001
B2-G1'	50	-.084	- .588	.556	15	1	3.742	<0.001
B2-B1'								
W-G1'	171	.308	4.015	<0.001	84	.159	1.449	.147
W-B1'	23	.458	2.147	<0.05	8	.619	1.638	.102
G1'-B1'	23	.490	2.297	<0.05	8	.833	2.205	<0.05

	Females to Others				Others to Females			
Seasons	**n**	**r_s**	**Z**	**p**	**n**	**r_s**	**Z**	**p**
SWIPE								
G1-B1	207	.226	3.250	<0.01	62	-.034	- .262	.793
G1-G2	100	-.032	- .314	.754	28	.856	4.447	<0.001
G1-B2	50	-.020	- .143	.883	15	.906	3.391	<0.001
G1-W	207	.335	4.802	<0.001	62	.183	1.429	.153
G1-G1'	171	.352	4.586	<0.001	50	.412	2.885	<0.01
G1-B1'	23	1	4.690	<0.001	8	1	2.646	<0.01
B1-G2	100	.179	1.778	.075	28	.265	1.376	.169
B1-B2	50	-.053	- .368	.713	15	-.105	- .391	.696
B1-W	207	.133	1.915	.056	62	.159	1.240	.215
B1-G1'	171	.261	3.397	<0.001	50	.136	.951	.342
B1-B1'	23	.938	4.397	<0.001	8	.833	2.205	<0.05
G2-B2	50	-.053	- .368	.713	15	-.071	- .267	.789
G2-W	100	.078	.773	.440	28	-.267	-1.389	.165
G2-G1'	100	.419	4.165	<0.001	28	.210	1.090	.276
G2-B1'	23	.938	4.397	<0.001	8	.714	1.890	.059
B2-W	50	-.053	- .368	.713	15	-.159	- .594	.553
B2-G1'	50	-.020	- .143	.886	15	-.071	- .267	.789
B2-B1'								
W-G1'	171	.141	1.844	.065	84	.118	1.075	.282
W-B1'	23	.829	3.886	<0.001	8	.625	1.654	.098
G1'-B1'	23	.938	4.397	<0.001	8	.708	1.874	.061
REST IN CONTACT								
G1-B1	207	.036	.501	.610	62	.187	1.464	.143
G1-G2	100	.126	1.258	.208	28	.012	.064	.949
G1-B2	50	.419	2.811	<0.01	15	.513	1.919	.055
G1-W	207	.172	2.464	<0.05	62	.272	2.128	<0.05
G1-G1'	171	.407	5.307	<0.001	50	.225	1.578	.115
G1-B1'	23	.938	4.397	<0.001	8	.833	2.205	<0.05
B1-G2	100	-.038	- .377	.707	28	.073	.378	.706
B1-B2	50	-.109	- .729	.466	15	.785	2.939	<0.01
B1-W	207	-.062	- .890	.374	62	.337	2.630	<0.01
B1-G1'	171	.092	1.200	.230	50	.484	3.390	<0.001
B1-B1'	23	-.151	- .709	.478	8	.560	1.480	.139
G2-B2	50	.740	4.962	<0.001	15	-.133	- .496	.620
G2-W	100	.373	3.707	<0.001	28	.274	1.425	.154
G2-G1'	100	.298	2.963	<0.01	28	.581	3.018	<0.01
G2-B1'	23	-.151	- .709	.478	8	.560	1.480	.139
B2-W	50	-.005	- .032	.975	15	.619	2.316	<0.05
B2-G1'	50	.143	.960	.337	15	.547	2.047	<0.05
B2-B1'								
W-G1'	171	.453	5.903	<0.001	84	.389	3.546	<0.001
W-B1'	23	-.164	- .771	.441	8	.560	1.480	.139
G1'-B1'	23	-.178	- .883	.405	8	.500	1.323	.186

(N.B. Most Cheek/Head Rub values were zero, and were therefore not included. Also, the Females with B2 values were not the same as those with B1' values, so correlation was not possible)

Table 4.10.j: Comparison of Yearly Behaviour Initiated and Received (n=45, 52). A significant result, using a Mann-Whitney U-test, indicates that the (ranked) rate of behaviour initiated by breeding Females to other cats is different from the (ranked) rate initiated by other cats to breeding Females.

Behaviour	**U**	**Z**	**p**		
Follow	946.5	-1.139	.255		
Approach	1011	- .616	.538		
Evade	978	- .875	.381		
Cheek/Head Rub	899	-1.738	.082		
Body Rub	868	-1.805	.071		
Close Sniff	1072.5	- .149	.882		
Groom	1055.5	- .317	.751		
Swipe	797.5	-2.384	<0.05	*	(rate to others>by others)
Rest in Contact	1005.5	- .665	.506		

Table 4.10.k: Kruskal-Wallis Statistics for the Rates of Focal Behaviour over Reproductive Seasons. A significant result means that the (ranked) seasonal rates of behaviour are different. The seasons with the highest rates are indicated, but are not statistically significant except in the context of the whole set of seasons (for this test).

Behaviour	df	n	H	p		Top Ranked
FEMALES TO OTHERS						
Follow	6	42	5.433	.490		W, G1
Approach	6	42	5.922	.432		B1, G1
Evade	6	42	4.832	.566		W, G1
Cheek/Head/Rub	6	42	8.644	.195		G1, B1
Body Rub	6	42	7.932	.243		G1, B1, W
Close Sniff	6	42	2.367	.883		G1, B1, W
Groom	6	42	4.546	.603		W, G1
Swipe	6	42	6.640	.356		W, B1, G1
Rest in Contact	6	42	9.044	.171		W, G1, G1'
OTHERS TO FEMALES						
Follow	6	52	10.805	.095		W, G1'
Approach	6	52	21.366	<0.01	**	B1, G1
Evade	6	52	16.222	<0.05	*	W, B1
Cheek/Head/Rub	6	52	3.165	.788		W, G1'
Body Rub	6	52	3.285	.772		W, G1'
Close Sniff	6	52	12.036	.061		W, G1'
Groom	6	52	21.841	<0.01	**	W, G1'
Swipe	6	52	9.241	.161		W, G1'
Rest in Contact	6	52	13.280	<0.05	*	G1', W

N.B. Ranks refer to reproductive seasons; W = Winter, G = Gestation, B = Breeding; 1 refers to the first litters of 1988, and 1' to the first litters of 1989.

Table 4.10.1: Correlations Across Seasons Between Focal Behaviour Patterns. A significant result indicates that, across the reproductive seasons and dyadic combinations, the ranks of the behaviour rates are linearly related. For example, breeding Females Follow and Approach specific other cats in specific seasons with similar (relative) rates for the two behaviour patterns. Note again that careful interpretation of significance levels is required with so many correlations.

	By Females to others (n=42)				By others to Females (n=52)			
Behaviour	r_s	Z	p		r_s	Z	p	
Foll-Appr	.370	2.368	<0.05	*	.482	3.440	<0.001	***
Foll-Evade	.148	.947	.344		.222	1.588	.112	
Foll-C/H/R	.310	1.984	<0.05	*	.232	1.656	.098	
Foll-B/Rub	.475	3.039	<0.01	**	.424	3.027	<0.01	**
Foll-C/Snf	.438	2.805	<0.01	**	.353	2.523	<0.05	*
Foll-Groom	.383	2.454	<0.05	*	.199	1.420	.156	
Foll-Swipe	.127	.816	.415		.388	2.770	<0.01	**
Foll-Rest/C	.409	2.618	<0.01	**	.126	.897	.370	
Appr-Evade	.212	1.358	.175		.469	3.351	<0.001	***
Appr-C/H/R	.264	1.690	.091		.456	3.259	<0.01	**
Appr-B/Rub	.535	3.429	<0.001	***	.502	3.586	<0.001	***
Appr-C/Snf	.581	3.721	<0.001	***	.702	5.010	<0.001	***
Appr-Groom	.447	2.860	<0.01	**	-.014	-.098	.922	
Appr-Swipe	.174	1.113	.266		.223	1.625	.104	
Appr-Rest/C	.405	2.592	<0.01	**	.319	2.280	<0.05	*
Evade-C/H/R	.157	1.003	.316		.180	1.289	.198	
Evade-B/Rub	.160	1.027	.304		.229	1.638	.102	
Evade-C/Snf	.286	1.831	.067		.432	3.086	<0.01	**
Evade-Groom	.353	2.263	<0.05	*	.188	1.339	.181	
Evade-Swipe	.358	2.294	<0.05	*	.348	2.486	<0.05	*
Evade-Rest/C	.273	1.748	.081		.146	1.040	.298	
C/H/R-B/Rub	.630	4.033	<0.001	***	.528	3.770	<0.001	***
C/H/R-C/Snf	.370	2.369	<0.05	*	.387	2.762	<0.01	**
C/H/R-Groom	.384	2.458	<0.05	*	.044	.311	.756	
C/H/R-Swipe	.483	3.090	<0.01	**	.118	.846	.398	
C/H/R-Rest/C	.204	1.306	.192		.085	.606	.544	
B/Rub-C/Snf	.324	2.075	<0.05	*	.395	2.824	<0.01	**
B/Rub-Groom	.279	1.785	.074		.276	1.973	<0.05	*
B/Rub-Swipe	.149	.954	.340		.093	.664	.506	
B/Rub-Rest/C	.264	1.691	.091		.289	2.063	<0.05	*
C/Snf-Groom	.402	2.573	<0.05	*	.274	1.957	.0504	
C/Snf-Swipe	.527	3.377	<0.001	***	.345	2.461	<0.05	*
C/Snf-Rest/C	.338	2.164	<0.05	*	.408	2.911	<0.01	**
Groom-Swipe	.283	1.815	.070		.273	1.952	.051	
Groom-Rest/C	.623	3.988	<0.001	***	.404	2.883	<0.01	**
Swipe-Rest/C	.174	1.115	.265		.191	1.364	.172	

Table 4.10.m: Seasonal Actions by Females to Kittens. Significant results indicate differences among breeding Females in the seasonal rates of behaviour initiated to Kittens, using Kruskal-Wallis tests.

Behaviour	**df**	**n**	**H**	**p**	
Follow	6	77	4.752	.576	
Approach	6	77	21.264	<0.01	**
Evade	6	77	21.246	<0.01	**
Body Rub	6	77	9.673	.139	
Close Sniff	6	77	19.412	<0.01	**
Groom	6	77	26.044	<0.001	***
Swipe	6	77	14.708	<0.05	*
Rest in Contact	6	77	18.752	<0.01	**

considered, Males Followed more overall, and Females Body-Rubbed and Rested in Contact more (Table 4.10.h).

Each behaviour pattern underwent a correlation analysis over all seasons, both for activity rates by Females and those directed toward them. This analysis gave an intricate web of connections (Table 4.10.i), which varied between behaviour to breeding Females and behaviour by them. Each datum represented a particular dyad, allowing the comparison of the relationships over different reproductive periods. Focal Female behaviour followed generally the same pattern from season to season, in that Winter, Gestation and Breeding were linearly related. This did vary with the activity, and behaviour with less specificity (e.g. Approach and Follow, which could be part of any scenario, including the initiation of contact or agonism) showed more correlations between all seasons. The spring Gestations were often correlated, for Evade, all Rubbing, Sniffing, Grooming, Swiping and Resting; this would appear to indicate some stability in the initiation of interactions by breeding Females. Perhaps Females seek out the same partners yearly, based on previous interactions. The actions by others demonstrated far less yearly similarity, except in Rubbing and Swiping.

Unfortunately, it was difficult to examine yearly spring Breeding to the same extent, due to the cessation of watches in April, 1989. However, indications were significant for Rubbing, Sniffing, Grooming and Swiping between breeding Females and others; the interactions were particularly marked between the Females and past/present/future helpers and partners. In general, first Gestation was correlated with first Breeding and Winter; different Gestation periods were also associated in the year (e.g. G_1, G_2 and G_1'), as were successive seasons, such that Gestation was related to Breeding, and Breeding to a subsequent Gestation. Later Breeding attempts (B_2) showed few behavioural connections to any other season, except, occasionally, Winter.

Yearly totals were again tested for differences between rates initiated by Females and those by others to Females. Only Swiping showed a significant disparity, in that the rate to others was greater than the rate by others over all seasons and all Females (Table 4.10.j). Then, when seasons were compared, few significant differences existed, although the pattern of ranks showed consistency (Table 4.10.k). When all activities were compared (χ_r^2= 362.225, $p<0.001$, df= 8, n= 94), the rank order of behaviour rates was as follows: Approach > Rest in Contact > Close Sniff > Follow > Evade > Body Rub > Groom > Swipe > Cheek/Head Rub. As before, the significant Friedman's test statistic refers only to the comparison over the whole set, with the rank order provided only to elucidate on the more extreme ends of the ranking.

After examining the seasonal pattern of each separate behaviour, another correlation analysis was performed to look at clumping of different behaviour rates in different seasons. In this case, each datum point represents a season and a Focal Female,

and a significant result means that, in seasons when high levels of behaviour "x" were manifested, changes in the rates of behaviour "y" were linearly related. Generally, in the same seasons, Follow, Approach, Rest in Contact, Groom, Rub and Close Sniff all increased, while Close Sniff, Swipe, Evade and Groom were similarly inter-related (Table 4.10.l).

Females differed in their behaviour to Kittens, depending on the reproductive season (Table 4.10.m). The greatest amount of all common actions occurred in the Breeding period in which the Kittens were born and over the following Winter; Females also Approached Kittens in the Gestation period of the next year.

4.5.3. SEASONALITY SUMMARY

Monthly behaviour rates were inter-related with the exception of Rubbing, Grooming and Resting in Contact (which had more sporadic rates). Certain sets of behaviour patterns were correlated together in various months, and these sets changed with seasons. Generally, Follow, Approach, Rest in Contact, Groom, Rub and Close Sniff all increased in the same seasons, while Close Sniff, Swipe, Evade and Groom were also inter-related at specific times. Reproductive seasons were then examined, and a pattern of correlations connecting Winter, Gestation, Breeding and Winter was found (similar to the associations found in spatial relationships), especially for affiliative actions (e.g. Focal Female behaviour followed generally the same pattern from season to season, in that Winter, Gestation and Breeding were linearly related). Females interacted more with Kittens during the Breeding and Winter periods. Overall, there appeared to be seasonal changes in the behavioural repertoire of individuals, responding to the dynamics of mating and breeding, such that investigative actions were rife in the mating times, and certain activities occurred in clusters (whether in the winter, gestation or breeding). The social behaviour showed some evidence of seasonal and yearly stability.

4.6. OCCASIONAL OBSERVATION DATA

Two separate forms of Occasional data were recorded. The first was the Continuous collection of information in 1987, some of which served as the basis for behavioural definitions. This set of data was the sole measure reflecting on the 1987 reproductive season, and was therefore examined for general trends and indicators of relationships between the founding Adults. The second collection of data referred to those actions, normally recorded for Focal individuals, which occurred during Focal watches on

other animals. These then could act as a supplementary source of information regarding more rare behaviour patterns. The data were not used for most of the nine common activities.

This section starts with 1987 and the Continuously-recorded measures. Individuals showed differences in the rates of different behaviour, both initiated to and received from other cats (Figure 4.10.a). The two Males, Zac and Trossachs, initiated and received the highest rates overall, while Tessa had the second rank for Group A, and Wanda initiated, while Jenny received in Group B. Only Cheek/Head Rub, Close Sniff, Groom, Social Play and AlloNurse had large asymmetries across all individuals (Table 4.11.a); all activities except Social Play were initiated more than received by Adults. When activities were correlated to look for associations in the rates, only Approach, Paw, Groom, Social Play, Swipe and Vocalise showed significant linear relations (Table 4.11.b), all positive, and probably due to the set of actions displayed with Kittens.

Over all behaviour measured, each individual performed at a different rate; Zac mainly Approached (Jenny was the preferred partner) and was Body Rubbed (by Molly). Jenny Hissed and Growled (to Zac) and was Approached (by Zac); Calico Groomed (her son Carbonel) and Rested in Contact (with Laura and others), and she was Followed (by Carbonel); Wanda Groomed (Mulberry) and Rested in Contact (with Mulberry and others), while she was Groomed (by Mulberry's mother, Molly). Laura acted in a fashion similar to Wanda, but was Groomed by Wanda; Molly also Groomed (Mulberry) and Rested in Contact (with Laura and others), but she was Approached (by Mulberry) and Evaded (by Zac) more. Daisy had low interaction rates, of which she Hissed and Growled the most (to Laura) and received Social Play (from Carbonel and Dijon).

As for Group A cats, Trossachs had high general Vocalisation and Spray-Mark rates, and he was Swiped (by Tessa). Katrina Evaded (Trossachs) and was Followed (by Trossachs and Poppy); Becky Hissed and Growled (at Tessa) and was Followed (by Poppy). Tessa Evaded and Swiped (Trossachs), and she was Followed (again, by Trossachs); Pansy Evaded (Trossachs, Tessa and Poppy) and was Body Rubbed (by Brigit). And Poppy Followed (Becky) and was Hissed and growled at by Becky. When each behaviour was considered separately, Males typically performed at the highest rates, except for Resting, Rubbing, Grooming, Playing and, of course, Nursing, activities which were predominantly the domain of Females.

Insofar as it was possible to examine seasonality, relationships, for most Adults, remained consistent over the year, and behaviour rates were related for most seasons. A few Females showed discrepancies from the overall pattern, in that Wanda was more "amicable" (increases in Rubbing, Grooming, etc.) in the Communal period, when most Group B Females were caring for a pooled litter (Calico and Molly, plus help from

Figure 4.10.a

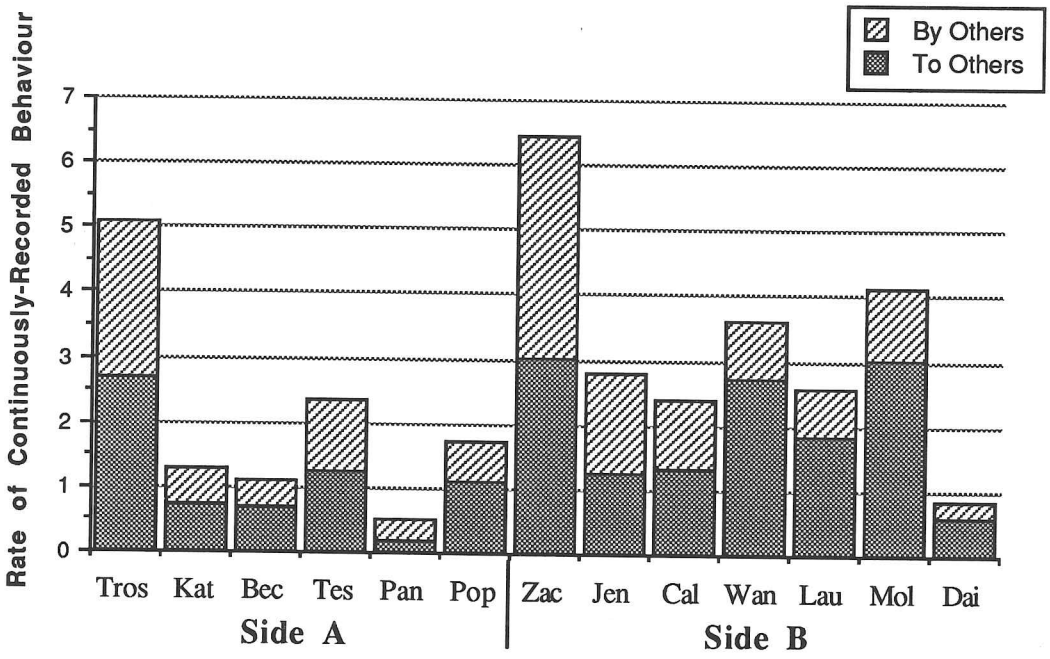


Figure 4.10.a: The rates of behaviour, from Continuous recording in 1987, for each Focal Adult individual. Both behaviour patterns directed to other cats and those received from others are included. "To Others" refers to rates initiated by the Focal animal, and "By Others" refers to rates received by the Focal individual.

Table 4.11.a: Wilcoxon Test Statistics Comparing Behaviour Initiated and Received. A significant result indicates an asymmetry in the (ranked) rate of behaviour initiated and received by Adults. For example, cats that initiated high rates of Cheek/Head Rubs did not receive similar rates from other cats.

Behaviour	**n**	**Z**	**p**		
Follow	12	- .628	.530		
Approach	11	- .222	.824		
Evade	13	- .909	.363		
No	11	- .268	.789		
Cheek/Head Rub	8	-1.963	<0.05	*	(to others>by others)
Body Rub	11	-1.157	.247		
Close Sniff	12	-2.238	<0.05	*	(to others>by others)
Paw	10	- .361	.718		
Groom	9	-2.666	<0.01	**	(to others>by others)
Social Play	5	-2.032	<0.05	*	(by others>to others)
AlloNurse	6	-2.201	<0.05	*	(to others>by others)
Swipe	11	- .624	.533		
Ear Flat	9	- .479	.632		
Tail Lash	12	- .591	.555		
Bite	6	- .954	.340		
Vocalise: General	11	-1.112	.266		
Hiss/Growl	13	- .734	.463		
Brr/Purr	7	- .085	.933		

Table 4.11.b: Spearman Rank Correlation for Behaviour Initiated and Received. Significant probability levels indicate linearly related ranks between the rate of behaviour initiated versus that received by each Adult individual.

Behaviour	**n**	r_s	**Z**	**p**	
Follow	13	.175	.607	.544	
Approach	13	.752	2.605	<0.01	**
Evade	13	.397	1.376	.169	
No	13	.141	.489	.625	
Cheek/Head Rub	13	.505	1.750	.080	
Body Rub	13	.496	1.720	.085	
Close Sniff	13	.433	1.500	.134	
Paw	13	.622	2.156	<0.05	*
Groom	13	.740	2.564	<0.05	*
Social Play	13	.617	2.137	<0.05	*
AlloNurse	13	0	0	1	
Swipe	13	.869	3.009	<0.01	**
Ear Flat	13	.244	.845	.398	
Tail Lash	13	.233	.807	.420	
Bite	13	.186	.643	.520	
Vocalise: General	13	.655	2.305	<0.05	*
Hiss/Growl	13	.253	.876	.381	
Brr/Purr	13	-.354	-1.226	.220	

Table 4.11.c: Individual Differences in Behaviour Categories, Using a Kruskal-Wallis Test. A significant probability level means that individual cats differ in the (ranked) rates of initiated behaviour from each category.

Behaviour	Group	df	n	H	p	
INITIATED						
Contact	All	12	102	27.988	<0.01	**
Contact	A	5	31	1.227	.942	
Contact	B	6	71	17.747	<0.01	**
Agonism	All	11	97	25.845	<0.01	**
Agonism	A	4	26	.894	.925	
Agonism	B	6	36	11.892	.064	
Vocalisation	All	12	75	18.502	.101	
Vocalisation	A	5	24	5.515	.356	
Vocalisation	B	6	51	7.106	.311	
RECEIVED						
Contact	All	26	102	29.413	.293	
Contact	A	10	31	3.878	.953	
Contact	B	15	71	19.123	.208	
Agonism	All	16	53	23.380	.104	
Agonism	A	6	17	5.732	.454	
Agonism	B	9	34	12.810	.171	
Vocalisation	All	19	74	22.943	.240	
Vocalisation	A	6	24	6.415	.378	
Vocalisation	B	14	51	12.242	.587	

Table 4.11.d: Wilcoxon Matched-Pair Tests on Behaviour Rates (Initiated versus Received). A significant probability level indicates that the (ranked) rates of initiated versus received behaviour are different; the direction of each significant difference is shown.

Behaviour	**Z**	**p**		
Follow	- .628	.530		
Approach	- .222	.824		
Evade	- .909	.363		
Neutral	- .268	.789		
Cheek/Head Rub	-1.963	<0.05	*	(to others>by others)
Body Rub	-1.157	.247		
Close Sniff	-2.238	<0.05	*	(to others>by others)
Paw	- .361	.718		
Groom	-2.666	<0.01	**	(to others>by others)
Social Play	-2.032	<0.05	*	(by others>to others)
AlloNurse	-2.201	<0.05	*	(to others>by others)
Swipe	- .624	.533		
Ear Flatten	- .479	.632		
Tail Lash	- .591	.555		
Bite	- 954	.340		
Vocalise (General)	-1.112	.266		
Hiss/Growl	- .734	.463		
Brr/Purr	- .085	.933		

Wanda and Laura), than in the preceding Gestation stage. Laura also had an increased number of amicable interactions, and decreased values for agonism and vocalisations, from the start of the Breeding season to the time of Communal care. Becky showed few consistencies between Gestation and Breeding, while Pansy became more "amiable" from the general Gestation time to Breeding. In this year, Poppy and Becky had a Communal litter, Tessa lost two litters through neglect, and Poppy tried to raise a late autumn litter with the help of Katrina and the younger cats. The presence of Kittens certainly seemed to enhance pro-social activities among Adults, especially those concerned with common litters. The connections between Gestation and Breeding interactions may have predisposed, or at least made possible, the joint breeding efforts seen.

To this effect, Wanda was probably involved in helping due to her relationship with Molly, rather than with Calico, who joined the group later; this was likely with Laura as well. In fact, there were few strong connections between Calico and the other Females until the subsequent year, when Wanda helped and later allomothered Calico's litter; Laura also went on to help Molly in 1989, but showed little interest in Calico or Wanda again. Daisy, who raised her Kittens alone, had few interactions with other Adults except those of an agonistic nature, and mainly exchanged actions with various Kittens and young cats. Of all possible interactants, Becky was mainly involved with Poppy, who returned this attention, reinforcing their cooperative efforts; in the meantime, the remaining Females in Group A focussed activities among themselves. Poppy also received quite a lot of initiations from the young cats surviving from her joint litter with Becky.

In summary, Males tended to be initiators of Approach, Close Sniff and Vocalisations, and they received Following, threat and defence gestures and Evasion; all these behaviour patterns are probably involved in mating processes. Females, however, Approached, Rubbed, Groomed and Nursed, and occasionally Pawed, Swiped and Evaded; these activities are more concerned with maternal and social relationships.

Similar actions were lumped into broader categories, wherein Contact was the sum of Resting in Contact, all Rubbing, Close Sniffing, Pawing and Grooming, while Agonism included Swiping, Ear Flattening, Tail Lashing, Piloerection and Biting. All the different sounds were lumped to give the third area of Vocalisation. Of the three, Contact ranked highest in frequency, followed by Vocalisation and then Agonism ($\chi_r^2 = 2.774$, $p = .250$, $df = 2$, $n = 36$), although the differences were not significant. When the three were compared using Spearman correlation over all dyads, Contact and Agonism rates increased together ($r_s = .349$, $Z = 2.209$, $p<0.05$, $n = 41$), as did Agonism and Vocalisation ($r_s = .625$, $Z = 4.002$, $p<0.001$, $n = 42$). Cats may well have been more irritable to familiar individuals or due to unsolicited attention (such as during "courting"), while many Vocalisations (e.g. Meow, Yowl, Hiss and Growl) were probably linked to Agonistic

encounters and relationships. Contact and Vocalisation were not linearly associated (r_s= -.068, Z= -.515, p= .607, n= 58).

Individuals were compared for the rates of each category that they initiated (Table 4.11.c); Group A cats did not differ significantly, but Group B cats showed diversity in the Contact rates, such that Wanda initiated most, and Daisy and Jenny initiated the least. When all individuals were considered, Contact and Agonism were both significant, with Wanda still the most Contact oriented (Trossachs and Pansy were the least overall) and also the most Agonistic (Becky and Pansy had the lowest scores). Cats were also compared for individual differences in rates of received behaviour, but these showed no significant values (Table 4.11.c).

When seasons were again considered, based on the rates of each behaviour category, the general finding was that different individuals acted differently in the seasons, depending on the precise circumstances; Males and Females had high Agonism and Vocalisation levels to one another during Gestation, with occasional peaks in Contact. Females continued to show a lot of Agonism to Males after the birth of Kittens; all the Females involved in Kitten-rearing showed the highest rates of Contact and Vocalisation during the Communal period (except with uninvolved Adults), and usually Agonism was at depressed levels. Non-breeding and Solitary cats were less focussed on the Breeding season, such that Males were quite active during Gestation (although Zac took interest during the Kitten period too), and the remaining Females varied with each dyad, and often peaked in Contact in the Winter, when cats congregated in common resting places.

Finally, all behaviour was pooled for an overall interaction rate over the observation period; the two Males, as with other tests, were the highest ranked for all actions (χ_r^2= 127.321, p<0.001, df= 13, n= 48), followed by Tessa (Group A) and Wanda (Group B). Behaviour initiated and received showed few changes from this position, except that Jenny was the second ranked recipient in Group B. Each activity was subjected to Wilcoxon tests, for initiation versus reception by each cat (Table 4.11.d); Cheek/Head Rubbing, Close Sniffing, Grooming and Nursing were all initiated at greater rates (and mainly to Kittens), while Social Play was received more. Doubtless, this was due to the influence of Kittens and the types of behaviour surrounding their presence. Approach (p<0.01), Paw (p<0.05), Groom (p<0.05), Social Play (p<0.05), Swipe (p<0.01) and Vocalise (p<0.05) were all positively correlated for rates initiated and received over all individuals (n=13), such that high initiators also received more.

The results of this more rudimentary analysis on 1987 behaviour seems to support the general findings from the 1988-89 Focal data collection examined in previous sections; Males were involved in a lot of behaviour, as initiators for presumably reproductively motivated actions, and as recipients of Female social attention. Females were mainly concerned with maternal activities in the Breeding periods, and spent other

time engaged in the apparent maintenance of social bonds, which may facilitate helping and Communal care when Kittens are born.

The second form of Occasional data concerned additional observations, especially of the more obvious but rare behaviour patterns, during the Focal watch period from January 1988 to April 1989. These measures were not commensurate with the other Focal data, as they recorded actual frequencies, and not the 30-second intervals used in One-Zero sampling. Therefore, they are supplemental, and act as a way of fleshing out the meagre Focal sightings of infrequent activities. Some opportunistic information was previously used in earlier sections of the chapter, when discussing the relevant actions, and the remainder is given here.

Mounting was discussed, using all possible sources of data, in Section 4.4.2. Focal samples recorded 39 Mounts, while Occasional observation noted another 89; in total, Adults performed 103 of these (80%) and Juveniles the remainder. All Juvenile Mounts involved other Juveniles (Male and Female) and Kittens only, while Adults Mounted all possible others (Adult, Juvenile and Kitten Females, Juvenile Males), with less interest in Kittens. Most Copulation and the attendant Female Response (rolling, yowling, swiping and self-grooming) was seen opportunistically, and occurred in all but Kittens and other Males. In Group A, Trossachs performed the same proportion of Mounts, whether Focal or not (71 and 73%); Zac, on the other hand, was responsible for 56% of Focal Mounts and only 34% of the others. This was probably due to the general tendency for younger Group B Males to lurk out of the main area, so that their Focal watches were reduced in number and taken whenever possible (and less at random). Rolling was a non-Focal behaviour and has been fully discussed earlier (Section 4.2.2), as were lordosis and other oestrus manifestations (Section 4.4.1).

Agonistic acts such as Ear Flatten, Tail Lash, Bite and Piloerect (Dards 1979) were not recorded generally, as they were barely noticeable when non-Focal. Fighting, however was more obvious. Only 8 Fights were seen Focally, while 38 were recorded in addition. Over half were Male-Male (54%), followed by Female-Female (24%), Female-Male (11%) and Male-Female (4%); for a few (n=3), only one animal was known, and these have not been assigned sex-classes. Zac was by far the most active in this behaviour, and accounted for 63% of all Fights, all initiated by him and mainly toward younger Males and Trossachs (the Adult Male from the other group). Jenny fought with other Adult Females (9%), Calico with maturing Juveniles (9%), and Poppy received aggression from her peers in Group A (7%); other individuals had only occasional Fights. Often Male-Male Fights would spark off aggression among the Females (also in Dards 1979), usually toward the fighters, but occasionally toward the nearest victim (especially Tessa to others, when adjoining Males were loudly involved in combat).

Vocalisations were another aspect noted opportunistically. An interesting feature was that Focal scores, although different in absolute scale, were the same by proportion; Group A gave 21% of Focal Meows, and 20% of non-Focal ones. They gave 52% of Focal Yowls and 54% of the Calls, versus 58% and 54% respectively of non-Focal Yowls and Calls. The same was true for proportions offered from each sex; Males consistently Meowed (13%), Yowled (75%) and Called (54%), whether Focal or not. The quieter sounds were not recorded occasionally, for fear of bias due to the less pervasive nature of the vocalisation.

Slightly less Scratching (e.g. of trees) was recorded non-Focally, but, as with Vocalisations, proportions were surprisingly uniform. Individuals varied between Focal and other scores, but overall trends did not; on Side A, Adults performed 75% of all Scratching (74% for non-Focal) for the group, while Adults on Side B did 72% (73% for non-Focal). Totals ranged from 3 (Catkin) to 52 (Molly), with a mean of 24 overall; Adult Females tended to contribute the most to this measure.

Scent-Marking was the last area in which opportunistic recordings were useful supplements. More detail is given in the following section (Section 4.7), but it is worth giving an overview here. Focal scores were generally higher, but some cats were only seen Marking in non-Focal periods (e.g. Catkin and Jenny). Trossachs was by far the most frequent sprayer, followed by Zac, Pishi and Doolittle (Figure 4.10.b); Females only contributed a total of 4 Sprays, from Molly (n=2), Jenny and Pippin. Zac Rubbed objects more, then Trossachs, Pishi and Dijon (Figure 4.10.c); Females performed a little more Rubbing (n=47), mainly from Becky and Jenny (only Katrina, Tessa and Wanda showed none). Spray-Marking frequency showed a seasonal pattern (Figure 4.10.d), typically peaking in late winter to early spring (mating) and mid-summer (Kitten period).

4.7. MARKING BEHAVIOUR

Scent-marking behaviour was an activity included in the Focal data collection because of its associations with territoriality and home ranges. The more confined nature of the study population meant that conventional techniques for the detection of ranges and territoriality could not be used, so scent-marking was analysed as a means of comparing this study group with others. Also, the general visibility of individuals allowed the examination of activities such as object Rubbing and Scratching. This section introduces the literature pertaining to scent-marking as the background for the data recorded in the present study. Different types of scent-marking are considered separately, including urine-spraying, tree-scratching, the deposition of faeces, and object-rubbing.

Figure 4.10.b

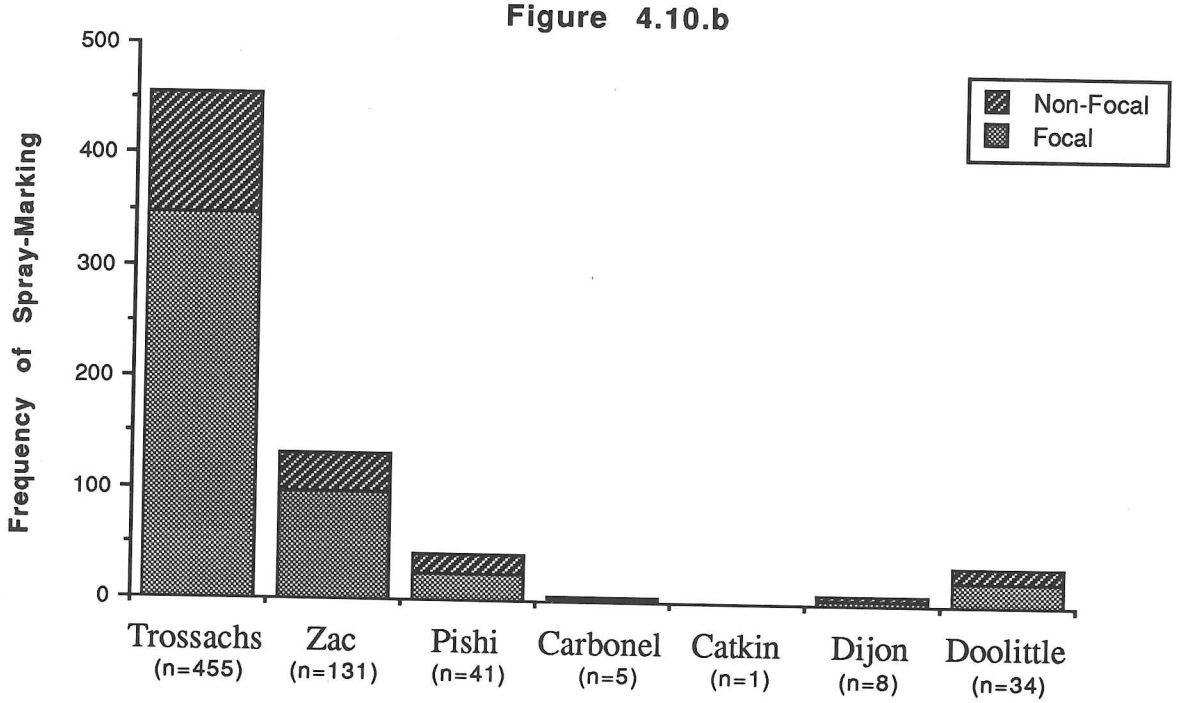


Figure 4.10.c

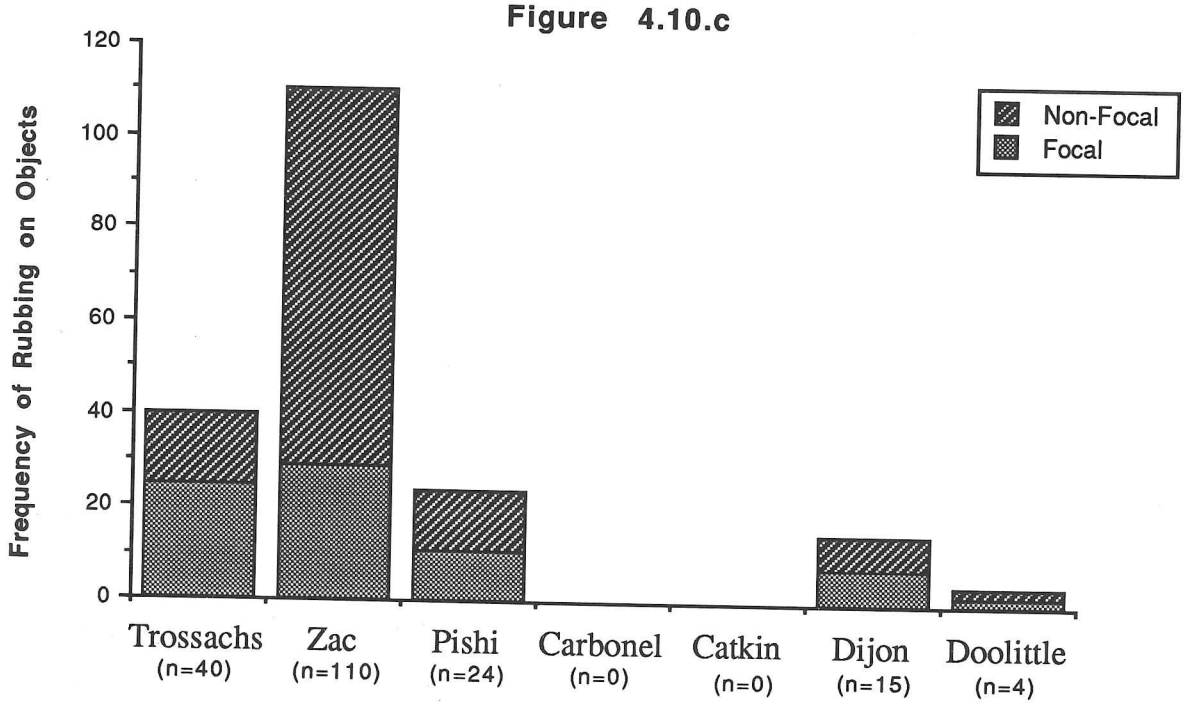


Figure 4.10: The frequency of scent-marking by Focal Males. Totals from both Focal observations and Occasional recordings are indicated. The sum of all occurrences is given by "n" for each Male. **(b)** Urine Spraying; **(c)** Object Rubbing.

Figure 4.10.d

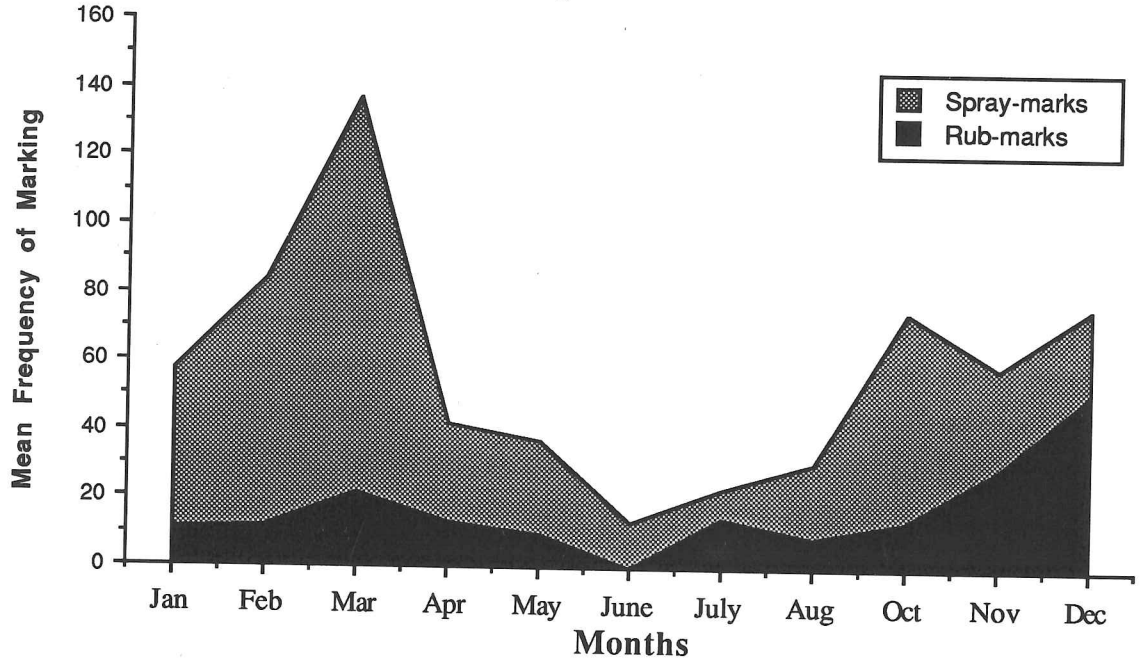


Figure 4.10.d: The seasonal distribution of Urine-Spraying and Object-Rubbing, given as the mean frequency for each month (for 1988 and 1989). Note that September is absent, due to a lack of observations in that particular month.

Most terrestrial mammals use olfaction as a primary means of communication, and this is particularly conspicuous in many carnivore species (Gorman & Trowbridge 1989). Odours are produced in most organs that secrete externally, including the sebaceous and apocrine sweat glands of the integument (Adams 1980; Gorman 1980; Gorman & Trowbridge 1989), salivary glands (Ewer 1968; Adams 1980), and accessory eye organs (Adams 1980). Urine, vaginal secretions and faeces are also used in many species (Smith 1977; Adams 1980; Gorman 1980; Macdonald 1980, 1985). In felids, the vomero-nasal organ, a specialised chemoreceptor, may help to discriminate urine and other closely-smelled odours; exercising all olfactory organs, it is possible for cats to detect low levels of complex mixtures, and even to distinguish individual odours by their varying composition (Dodd & Squirrell 1980).

Scent-producing organs in the cat are located on the cheeks, abdomen, paws, above the tail, and near the anus (Ewer 1968, 1973; Gorman 1980; Macdonald 1985; Gorman & Trowbridge 1989); secretion is controlled by the endocrine and nervous systems (Adams 1980). Secretions are placed on prominent objects and other individuals (Smith 1977; Gorman 1980; Macdonald 1980), with a technique known as "scent-marking". Many Felidae, including the domestic cat, are retromingent and urinate posteriorly (Ewer 1968, 1973; Corbett 1979; Macdonald 1980); this allows the deposition of urine mixed with either vaginal or anal gland secretions (Macdonald 1980), which is discussed below as "Spray-Marking". A second common way to deposit odour may be through scratching objects while exuding odorous secretions from paw glands, as is discussed further in the "Scratching" section.

The function of scent-marking is not fully known, although a number of hypotheses abound. The nature of the odour marks probably allows individual recognition, or at least, identification of the marker's sex or group membership; the frequency of marks may display some clue to status. The position of marks can convey spatial information; and the temporal pattern of scent-marking can potentially signal reproductive condition and temporal use of the home range (Gosling 1982; Macdonald 1985; McFarland 1987; Gorman & Trowbridge 1989; Passanisi & Macdonald 1990). Both urine and skin gland secretions of females seem to contain pheromones that advertise reproductive state to investigating males (Verberne & De Boer 1976; Gosling 1982). Social groups may give rise to a common group odour, based on a mixture of all members, especially in the presence of allomarking (particularly rubbing in cats) and the marking of common objects (Gorman 1980; Gorman & Trowbridge 1989). Many mammals may use odour as a means of demarcating territories (Macdonald 1985; Gorman & Trowbridge 1989); a territory has been defined by Ewer (1968) as "an area from which conspecifics are excluded by being attacked or threatened if they venture within its confines and it may or may not be coextensive with the home range". On the other hand, a home range is "an area

regularly traversed by an individual in its activities" (Morse 1980), and includes territories and, especially, undefended areas. In this sense, the domestic cat tends to occupy home ranges, and these may overlap extensively (Ewer 1968; Gorman 1980), precluding the designation of territory.

It has been noted that species with overlapping ranges tend to mark within the range, especially near the core area, and animals often mark paths as they move throughout the range (e.g. Eurasian badger and European otter: Gorman 1980; tiger: Smith et al. 1989). Whereas, strongly territorial species concentrate efforts at the territorial boundaries, as well as marking throughout, e.g. the placement of badger latrines at borders (Gorman 1980). Therefore, even marking patterns may help to elucidate the degree of species-specific territoriality. Gorman (1980) goes on to speculate that the two methods of marking have separate functions; marking throughout may serve to maintain familiarity with the home range and therefore act as a form of reassurance to the resident; boundary marking may be a specialisation to act as a warning or threat to potential intruders, communicating the presence of a resident and the edge of the territory.

There is little evidence that scent-marks actively deter intruders from entering an area (except in foxes and wolves: Macdonald 1985), but they could act as a warning mechanism, predisposing an intruder to yield in an encounter with the resident. The matching of scent-marks with their owners may allow intruders a means by which to assess potential competitors; territory holders are more likely to be challenging opponents, due to their dominant status and the pressure to maintain a hold on the present resources, and intruders might be advantaged by relinquishing claims in the presence of known residents (Gosling 1982; Gorman & Trowbridge 1989). In addition, territory holders, by allowing their identification with scent-marks, may benefit from non-escalated aggression whenever possible. This may offer a partial explanation for the common observation of scent marking during agonistic encounters (Gosling 1982). Rarely have cats been seen to leave or avoid an area after investigating marks, which lends strength to the explanation that they serve as information markers rather than as an active method of deterrence (Bateson & Turner 1988).

4.7.1. URINE SPRAY-MARKING

Spray-marking can be distinguished from elimination by orientation to a specific object and repetition on the same object (Macdonald 1980; Bateson & Turner 1988). In cats, it can also be recognised by the characteristic form, in which the marking individual (usually Male) backs up to an object, lifts its tail vertically, and directs a fine spray between its hind legs, accompanied by an intense quivering movement of the tip of the tail (Ewer 1968; Corbett 1979; Dards 1979; Leyhausen 1979; Bateson & Turner 1988).

Anal sac contents may be mixed with urine (Dards 1979) to create a characteristic and pungent concoction which may be distinguished from ordinary eliminated urine; anal sacs are paired organs found either side of the anus, opening to the rectum, which hold apocrine and sometimes sebaceous secretions (especially prevalent in domestic cats, lions and tigers)(Macdonald 1985; Gorman & Trowbridge 1989). Urine spraying is considered the predominant method of scent-marking in canids and many felids, including the domestic cat and tiger (Smith et al. 1989), as it can be performed rapidly and leaves apparently persistent olfactory cues.

It has been remarked that male cats, along with other carnivores (e.g. wolves, golden jackals, spotted hyaenas, red foxes, lions and dogs) show a high frequency of spray-marking after agonistic encounters (Dards 1979; Macdonald 1980). Adult male cats spray frequently, often while walking along the paths and boundaries of a range (Liberg 1981; Macdonald et al. 1987; McFarland 1987), and while hunting (Corbett 1979); adult females have been occasionally observed to spray, also while hunting and travelling along paths, but much less frequently than adult males (Panaman 1981; Natoli 1985).

Erect-spraying, on vertical surfaces, is a more common method, but spray can also be directed to the ground (squat-spraying), accompanied by treading motions with the paws (Bateson & Turner 1988). Spray marks are often directed onto conspicuous objects, such as grass tussocks (Corbett 1979), projecting twigs (Gosling 1982) and tree stumps (this study), which may lend strength to the argument that they have a function as a spatial marker. In tigers, the size and leaning angle of a tree may affect an individual's preferences for spraying (Smith et al. 1989); in this species, marking is considered the primary means for shaping and maintaining territorial boundaries, and tigers will deviate to mark or inspect particular sites (although they rarely retrace their steps to reinspect or respray).

Several recent studies have shown that adult cats can distinguish the urine of familiar and unfamiliar conspecifics (Natoli 1985); males sniff longer at the urine of oestrus females (Verberne & De Boer 1976) and fresh spray is smelled for longer periods than older marks (De Boer 1977). Passanisi and Macdonald (1990) tested responses to urine in a population of farm cats and confirmed earlier findings: adult males investigated all conspecific urine for longer periods; sprayed urine elicited more sniffing; and, sprayed urine from unfamiliar animals evoked longer investigations from all adults. Males seem particularly interested in the odours of strangers and reproductive females, perhaps displaying a tendency to "keep track" of any changing factors in the area; given the same urine, males sniff and "flehmen" more frequently than females (Verberne & De Boer 1976).

In the present study, including both Focal and Continuous observations, a total of 679 Spray-Marks were delivered by the cats; of these, only 4 were performed by

Females, and the remaining 675 (99%) by Males; this was a statistically significant difference (U= 1.5, Z= -3.939, $p<0.001$, n= 7 Males, 15 Females). All of these marks were yielded by Adult cats, at least 18 months old. Marks were unequally distributed between the two groups, in that Side A contributed nearly three times more Spray-Marks than Side B (497 to 182) despite the larger group size and the greater preponderance of Males in B; however, it was not significant over all individuals (U= 47, Z= -.939, p= .348, n= 10 Group A, 12 Group B). When only Zac and Trossachs, the principal Adult Males throughout the study, were considered, Trossachs was found to Spray much more frequently (χ^2= 179.14, df= 1, $p<0.001$), contributing 9.2 Spray-Marks per hour to Zac's 2.8 Sprays per hour. If marking frequency is linked to high dominance status, through the influence of androgens (Gosling 1982), then Trossachs might appear to be a more dominant Male, or at least a highly territorial individual, in the presence of a neighbouring potential competitor.

4.7.2. SCRATCHING

A variety of carnivore species have been observed to scratch and gnaw the bark of trees, leaving a visibly discernible area of damaged wood. One of the functions of scratching is the sharpening, cleaning and upkeep of claws (Hediger 1950; Bateson & Turner 1988). As well, wild cats are known to use "claw-sharpening" trees, which can serve as both visible and olfactory markers (Ewer 1968; Corbett 1979; McFarland 1987), due to the presence of scent glands on the interdigital membrane of each paw (Ewer 1973; Macdonald 1985). Felid species that regularly display this behaviour include the domestic cat, African and European wildcats, the bobcat and leopard; it has also been noted, to a lesser extent, in tigers, lynx and pumas (Hediger 1950; Ewer 1973; Smith et al. 1989). The same tree may be used repeatedly over time, as in the tiger (Smith et al. 1989), wolverine, domestic cat and bear (Ewer 1973), even by different individuals. Bears are seen to rub trees, especially with urine, which are located near active tracks (Reiger 1979; Macdonald 1980); it has been postulated that these marker trees designate favourite or habitual pathways, as in the brush-tailed opossum (Ewer 1968). In this study, two possible distribution patterns for the scratched trees were considered: either along the perimeter or along the clearly heavily used paths throughout the enclosure.

Overall, seven distinct types of tree were growing in the enclosure, with four species particularly common (Figure 4.11.a). Including both sides of the enclosure, a total of 167 trees was found, ranging in size from young saplings little more than an inch in diameter and six feet in height, to mature trees with trunks several metres in girth. The majority of trees were completely unmarked by Scratches, but most of those used as "Scratching posts" showed severe damage to the integrity of the bark (Figure 4.11.b).

Figure 4.11.a

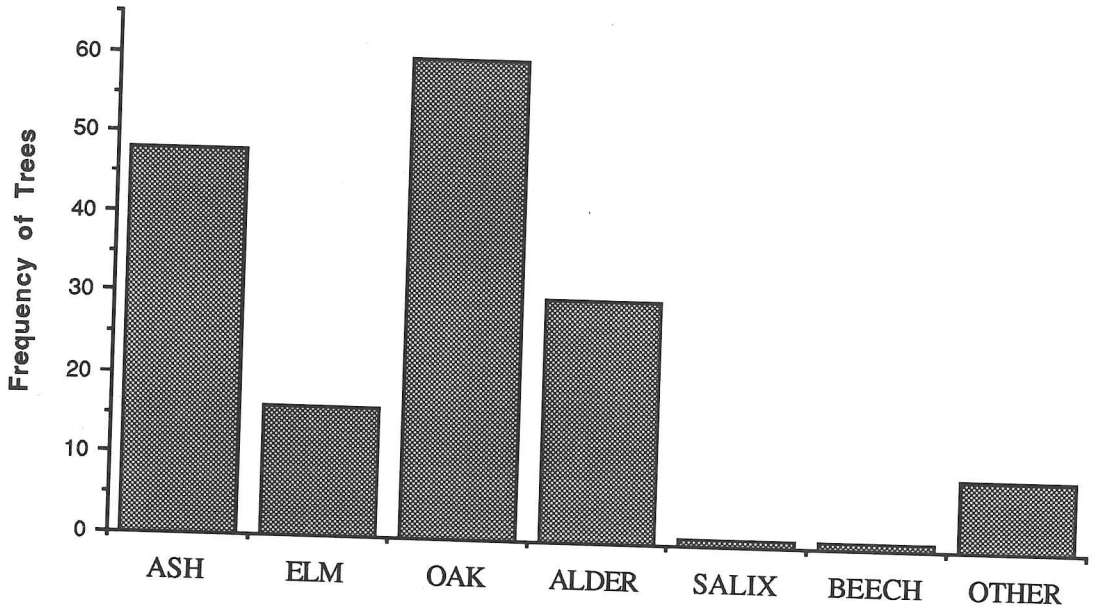


Figure 4.11.a: The distribution of tree types throughout the enclosure (both Sides A and B). The total number was 167 trees.

Figure 4.11.b

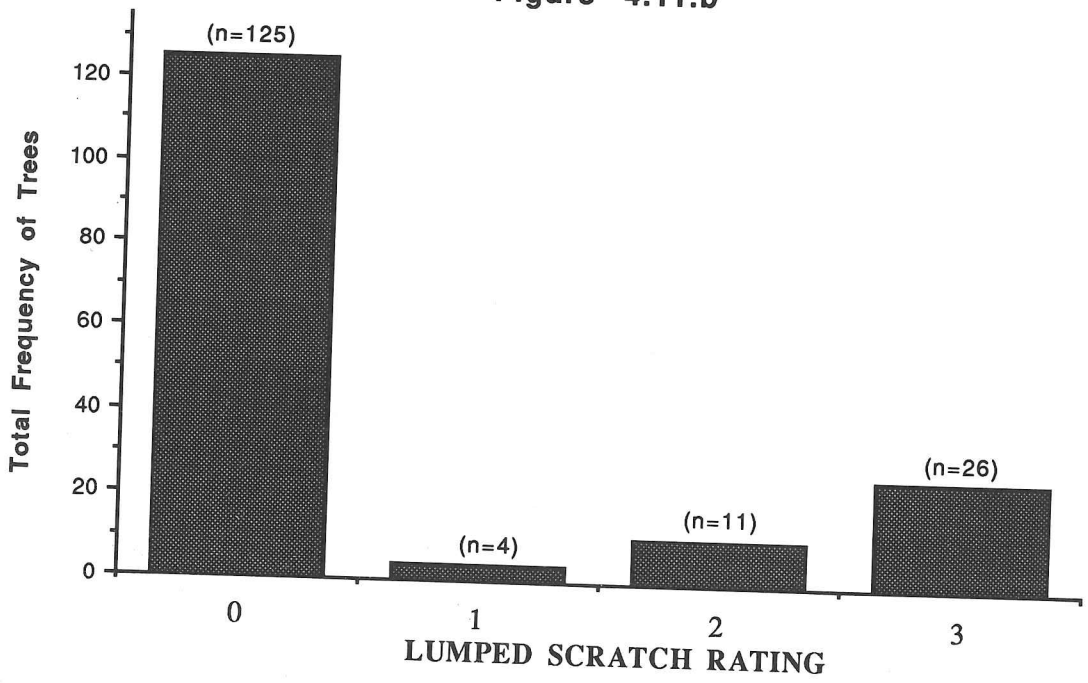


Figure 4.11.b: The distribution of Scratching intensity for all trees in the enclosure (both Sides A and B). "O" denotes an unscratched tree, scratching damage increases from "1" to "3".

Figure 4.11.c

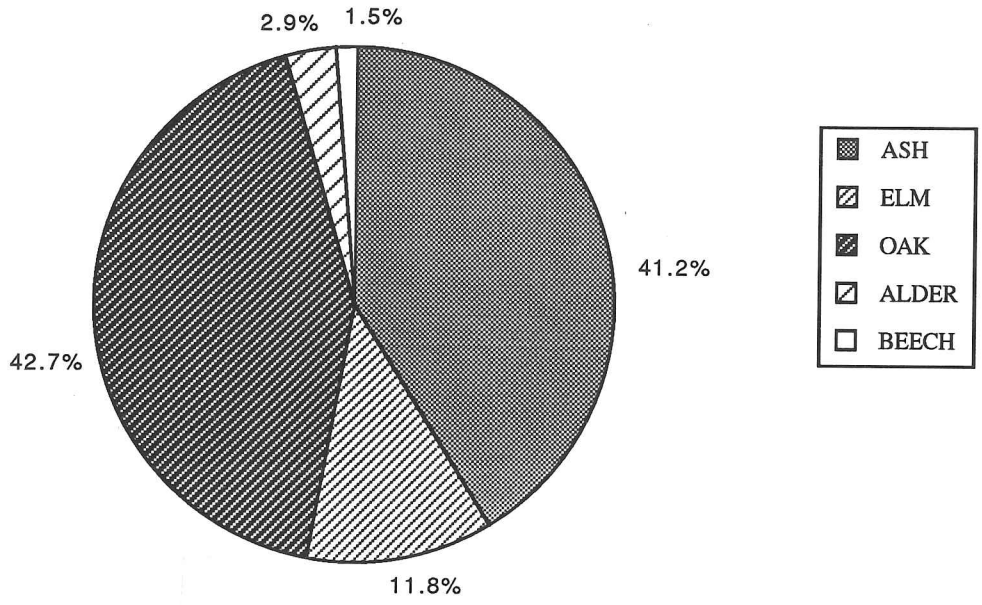


Figure 4.11.d

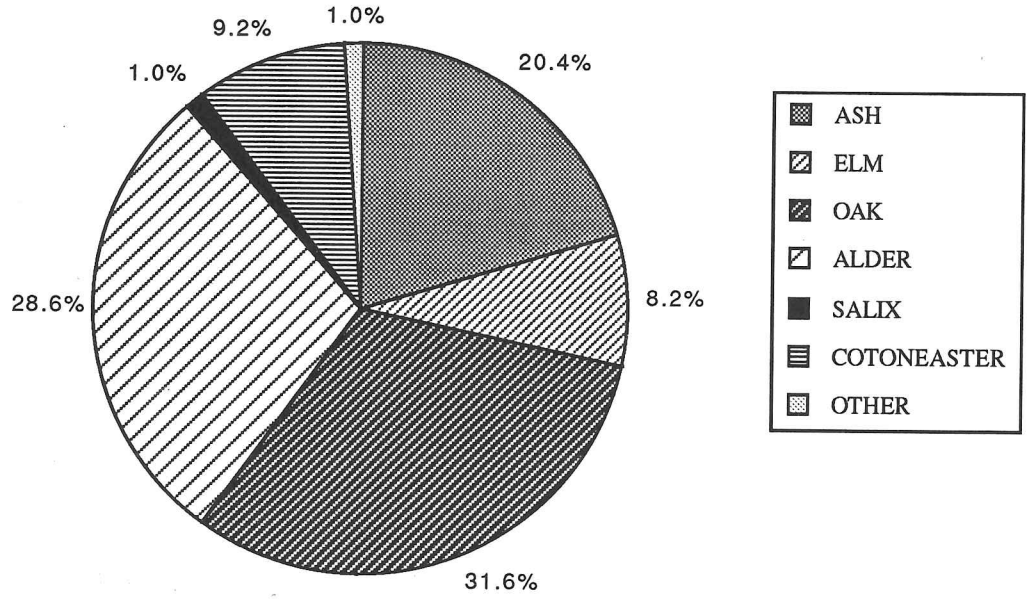


Figure 4.11: The distribution of tree types in the two sides of the study enclosure, expressed as proportions of the total number of trees per side. (**c**) Side A, total number = 69 trees; (**d**) Side B, total number = 98 trees.

Figure 4.11.e

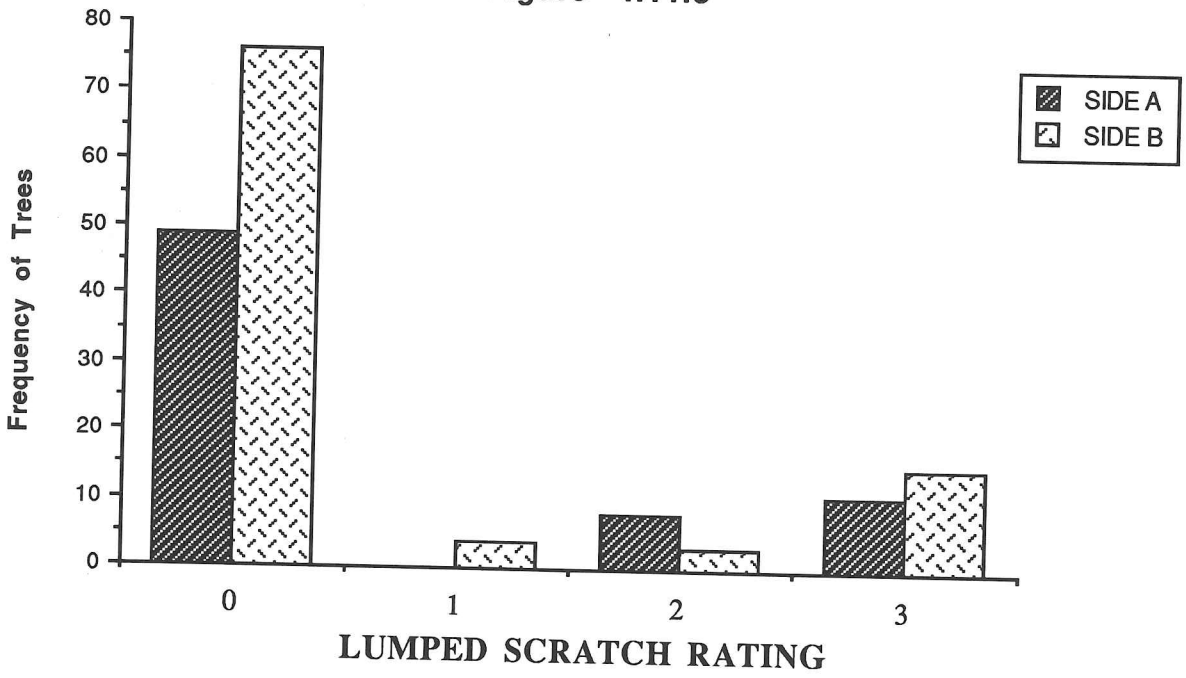


Figure 4.11.e: The distribution of Scratching levels for the two cat groups. The frequency of trees at each Scratch intensity is presented, ranging from the unscratched trees ("0") to the most scratched trees ("3").

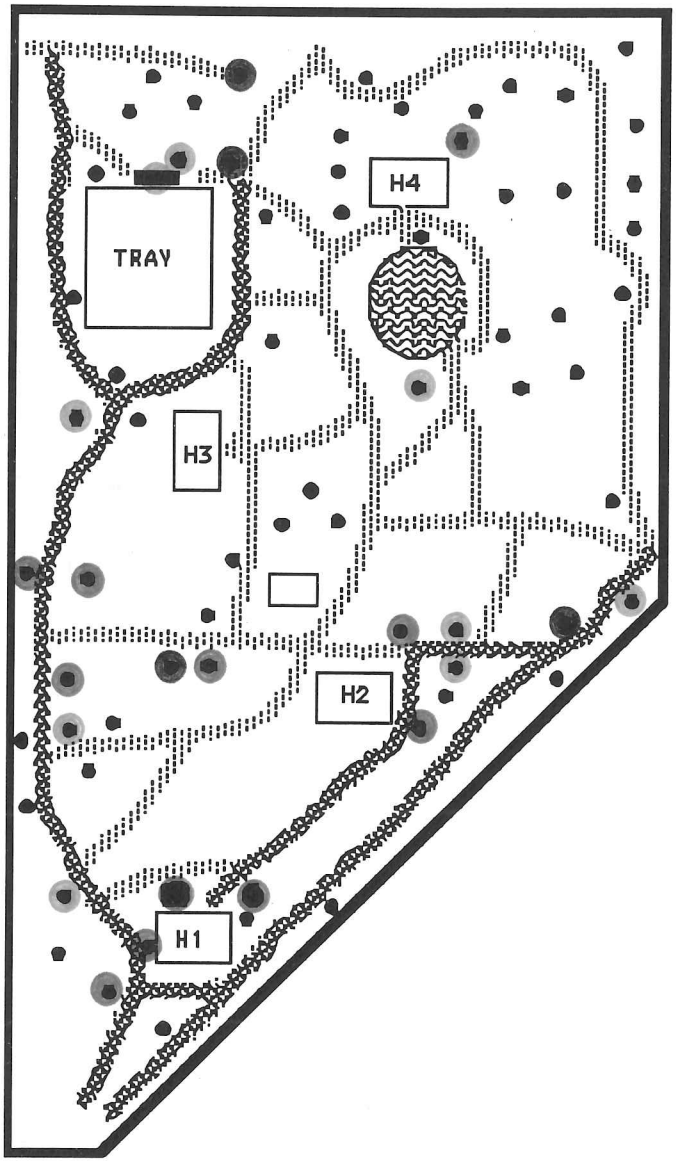


Figure 4.11.f.1: The Location of Scratched Trees in Side A of the Enclosure. Wooden shelters are marked as H1 to H4. Paths are indicated by thick lines, with more heavily-used routes in darker shading. Scratch use is denoted by colour, such that the most scratched trees (3-3+) are red, moderate scratching (2, 2-3) is in orange, low scratching (1, 1-2) is in yellow, a touch of scratching (0-1) is shown as green, and unscratched trees are simply black dots.

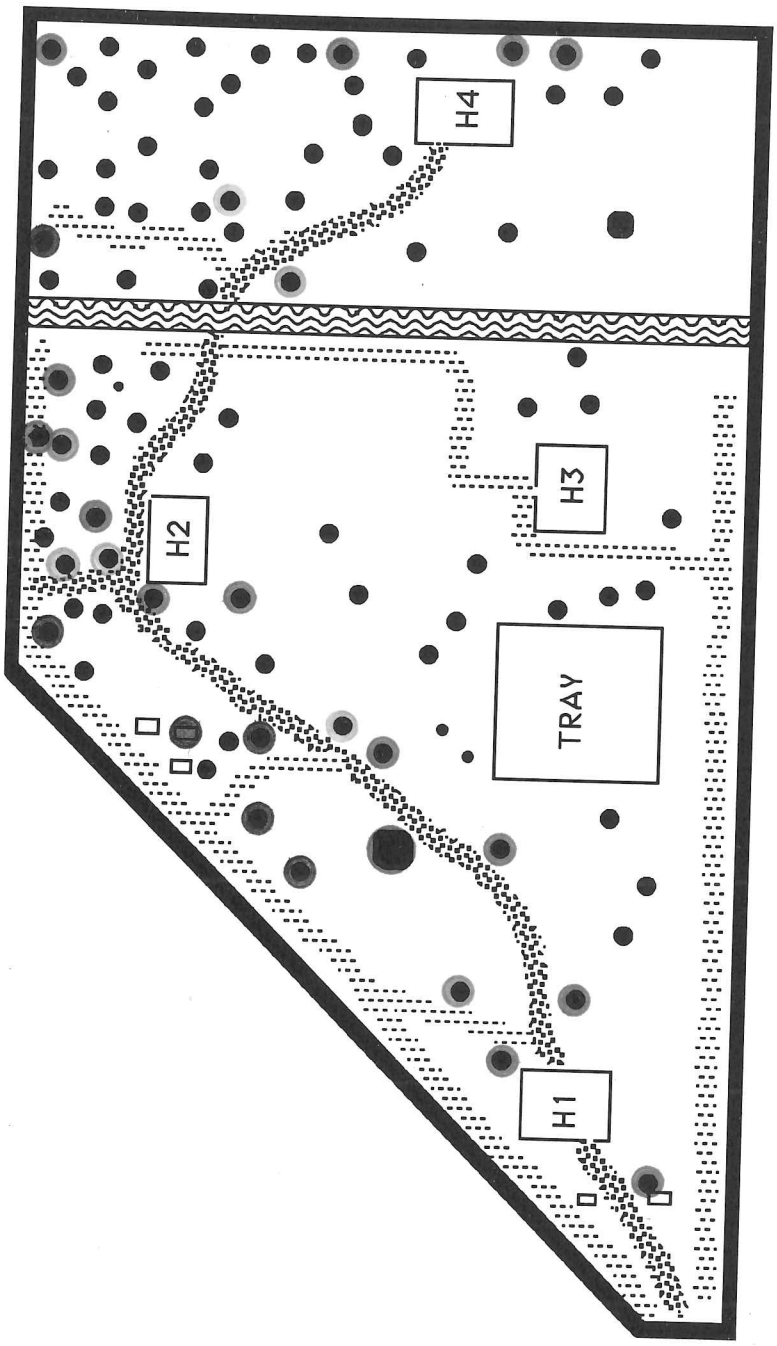


Figure 4.11.f.2: The Location of Scratched Trees in Side B of the Enclosure. Wooden shelters are marked as H1 to H4. Paths are indicated by thick lines, with more heavily-used routes in darker shading. Scratch use is denoted by colour, such that the most scratched trees (3-3+) are red, moderate scratching (2, 2-3) is in orange, low scratching (1, 1-2) is in yellow, a touch of scratching (0-1) is shown as green, and unscratched trees are simply black dots.

Figure 4.11.g

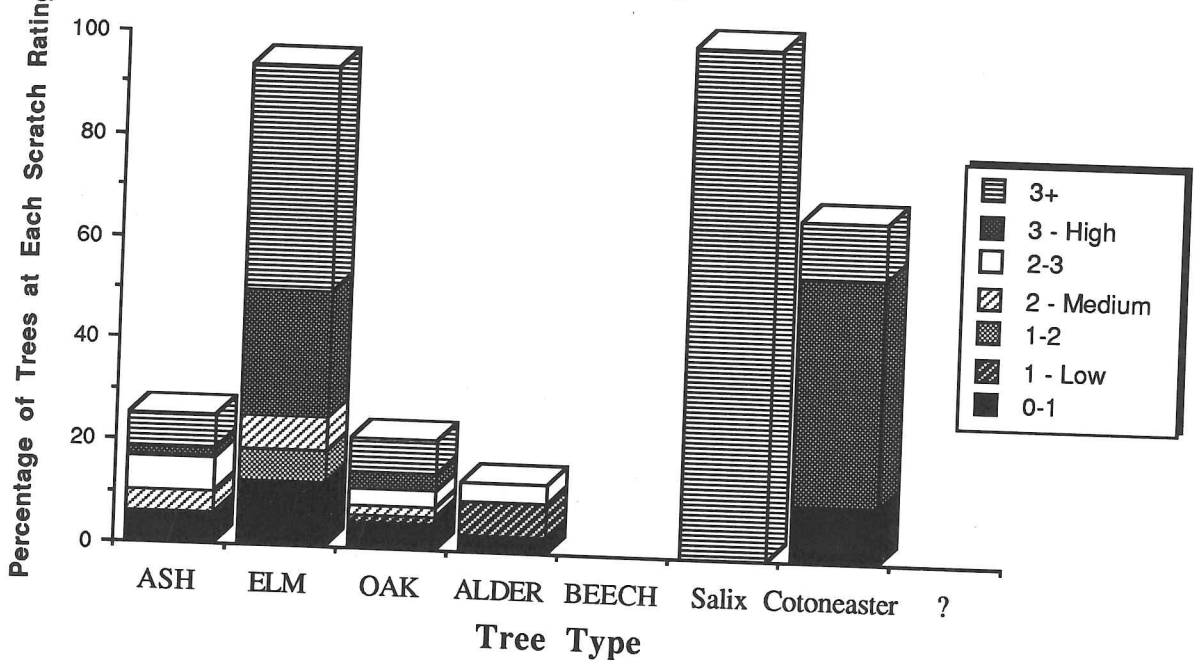


Figure 4.11.g: The Scratching levels on each tree type for the entire enclosure (both Sides A and B). Each Scratch category is included, from "0-1", or very light bark damage, to "3+", or the most shredded and damaged bark. The proportion of trees at each category is presented, with the total made up by unscratched trees (not shown). A three-dimensional plot is used to show the small numbers more clearly.

Figure 4.11.h

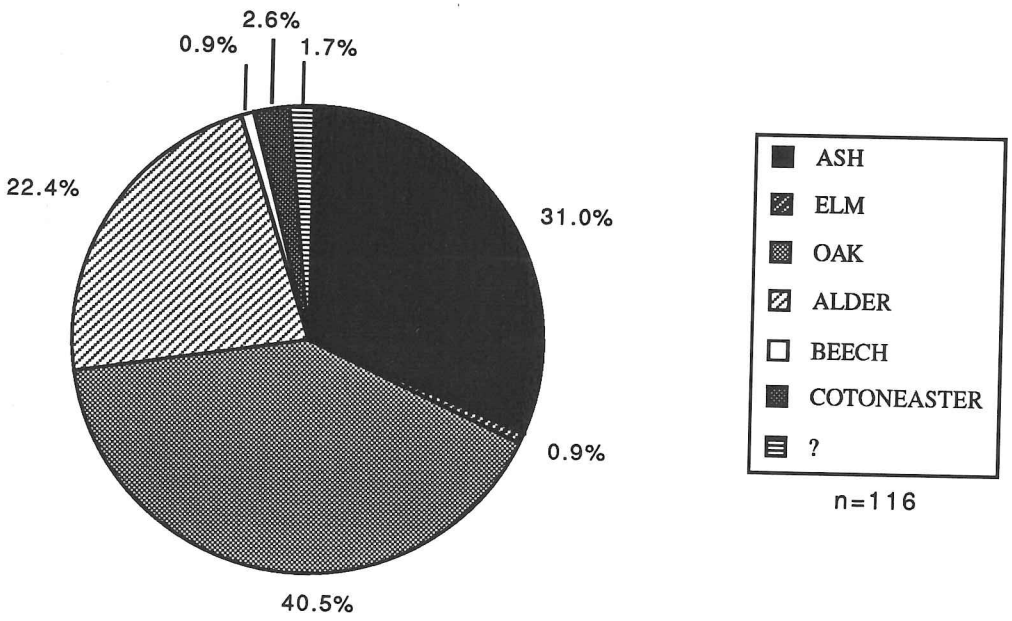


Figure 4.11.h: The proportion of each tree type making up the total number of unscratched trees in the enclosure (both Sides A and B). The question mark represents those trees (n=2) which were unidentifiable.

Figure 4.11.i

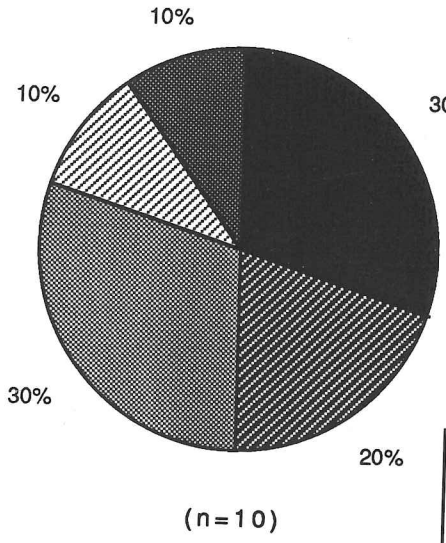
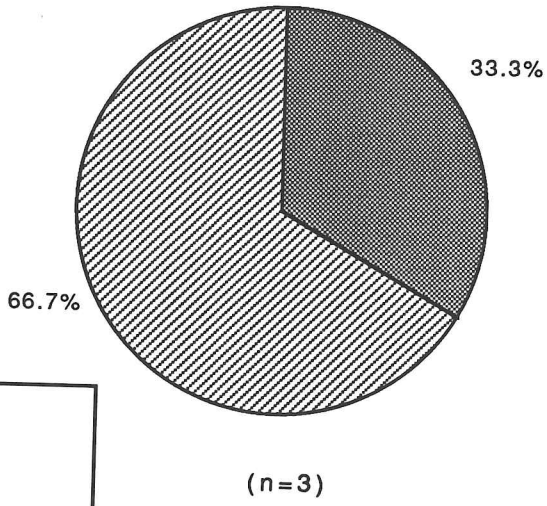


Figure 4.11.j



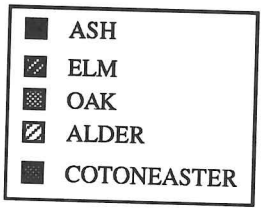


Figure 4.11.k

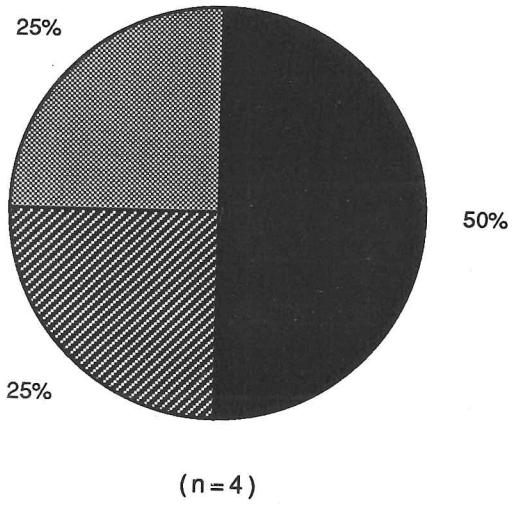


Figure 4.11.l

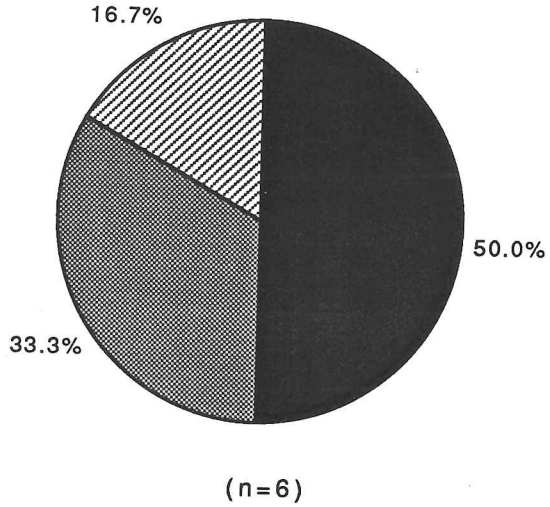


Figure 4.11: The proportion of each tree type making up the total number of scratched trees at each rating in the enclosure (both Sides A and B). The number of trees at each rating is given by "n". Only one tree was rated "1-2", and so was omitted. Higher ratings denote higher Scratching levels. (i) Trees at the 0-1 Scratch Rate; (j) Trees at the 1 Scratch Rate; (k) Trees at the 2 Scratch Rate; (l) Trees at the 2-3 Scratch Rate.

Figure 4.11.m

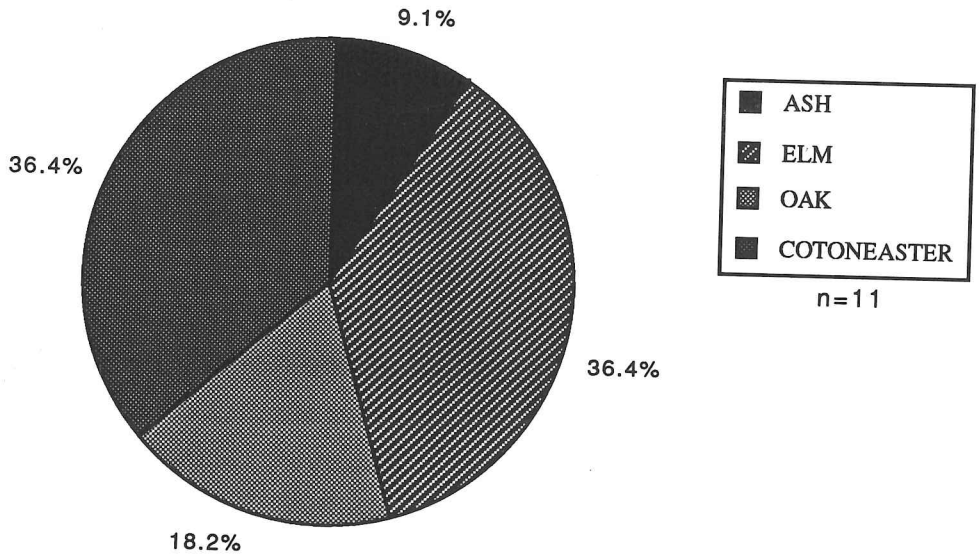


Figure 4.11.n

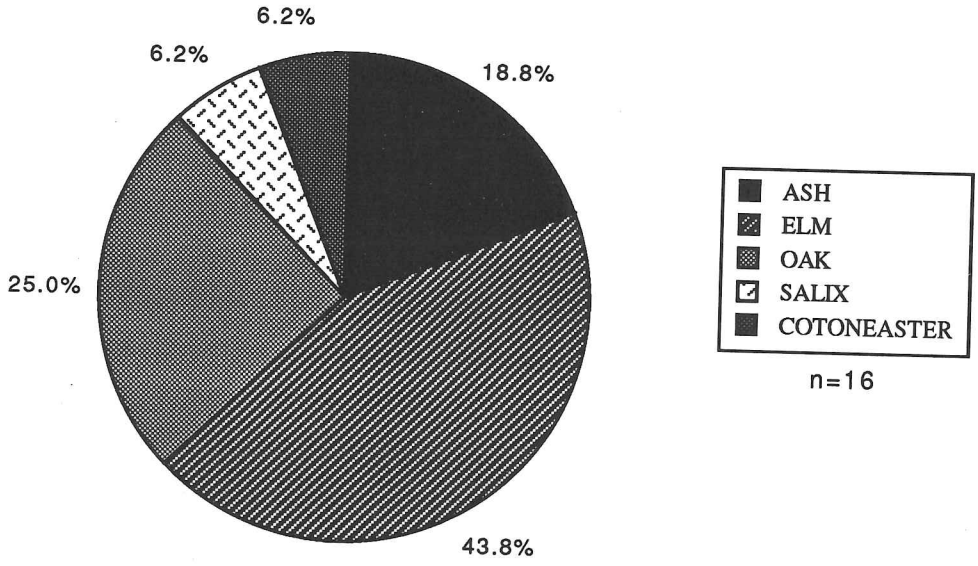


Figure 4.11: The proportion of each tree type making up the total number of scratched trees at each rating in the enclosure (both Sides A and B). The number of trees at each rating is given by "n". "3" and "3+" refer to the most highly scratched trees. (**m**) Trees at the 3 Scratch Rate; (**n**) Trees at the 3+ Scratch Rate.

Some differences were found between the two sides, both in tree composition (Figures 4.11.c & d) and in Scratch use (Figure 4.11.e).

The total tree distribution in each colony was examined to see whether there was a particular pattern to the Scratched trees. As Scratch-Marking is a well-documented territorial phenomenon (see above), perhaps the perimeter of each side was being Scratched more vigorously to signpost the presence of a resident. However, when the placement of Scratched trees was mapped out (Figure 4.11.f [1 & 2]), it became apparent that heavily Scratched trees were located primarily in the central part of the territory, along well-defined and much-used routes, and only rarely at the outer boundaries.

Even along the paths, there appeared to be a sporadic distribution of Scratched and unscratched trees, in that several unmarked trees were intermingled with heavily Scratched ones. Perhaps the intrinsic nature of the trees, their species and bark-type, influenced the choice of Scratching posts; hard, smooth-barked sorts might be less suitable, offering strong resistance to shredding forces. All the trees were then examined by species to see if, perhaps, a species-specific bark characteristic was being selected. Specific descriptions and species names were gained through consultation with P. Heavens (pers. comm.) and Mitchell (1988).

The Common ash (*Fraxinus excelsior*) has pale grey bark which is very smooth on young trees and which becomes thick interwoven ridges in old trees. The English elm (*Ulmus procera*) has dark brown bark which is deeply cracked into small square plates, and has small sprouts spreading from numerous burrs. The English oak (*Quercus robur*) grows with a few massive twisting low branches and lots of interior shoots and foliage; the bark is pale grey and closely fissured into short, narrow, vertical plates. *Alnus cordata*, the Italian alder, displays bark which varies from pale brown-grey to dull grey. The texture is smooth but blistered, with a few vertical fissures - shallow and wide. For an alder, this species has relatively dense foliage.

The three less-common tree species have the following characteristics: the Common beech (*Fagus sylvatica*) has smooth, silvery-grey bark, often slightly roughened and less often with rippled patches or a fine network of ridges; *Salix pentandra*, the Bay willow, shows brown-grey bark, finely fissured by narrow orange buff cracks; and the decorative pale grey-barked Cotoneaster (*Cotoneaster frigidus*), is originally from the Himalayas, short-boled, often leaning, with long vertical sprouts growing from the bole.

Two-thirds of all ash, oak and alder trees were left unmarked (Figure 4.11.g); those that were Scratched showed varying degrees of damage: ash and oak had frequent instances of intense Scratching, while alders were only moderately Scratched at most. All three species have relatively hard bark, often smooth or with vertical grooves; claws seemed unable to display much effect, especially on older trees. Alders seem particularly hard and "peely". Most elms, on the other hand, were Scratched to some extent; nearly half of all

elms (n=16) were placed in the highest category, showing large areas of shredded bark (Figure 4.11.g). Based on visual evidence, it appeared that elm bark was more easily pulled into strands and yielded an attractively soft Scratching substrate.

The Cotoneaster trees were similar to the elms in that the surface was frequently filamentous in appearance, after habitual Scratching had destroyed the integrity of the bark. Of the nine Cotoneasters, five were very highly Scratched and four hardly at all (Figure 4.11.g); the disparity is probably due to the placement of the trees on or away from heavily-used routes through the enclosure. The single beech tree was unscratched, while the willow was highly shredded.

If Scratch-damage categories are considered (Figures 4.11.h-n), oak, ash and alder made up the greatest proportion of unmarked trees ("0" Scratch rate); ash, elm and alder were the only contributors to the moderate categories ("2" and "2-3"); extremely Scratched trees ("3+") were nearly half elm (43.75%), with most of the rest contributed by ash (18.75%) and oak (25%). Using a Friedman's test, with tree type as "blocks" and Scratching as the matched factor, the differences were significant (in the pattern of Scratching) across tree types (χ_r^2= 23.636, p<0.01, df= 7, n= 8). If ash, oak and alder trees are classed as "hard-barked" based on their descriptions, and elm, Salix and Cotoneaster as "soft-barked", then Scratching damage can be compared using 2x2 contingency tables. Soft-barked trees were Scratched significantly more (considering any Scratching at all) (χ^2= 38.387, df= 1, p<0.001); and, when only Scratched trees were considered, soft-barked trees were Scratched significantly more at the highest rates, "3" and "3+" (χ^2= 7.557, df= 1, p<0.01). These results support the hypothesis that differential Scratching is due, in part, to the type of bark of the tree species. Location of tree also plays a major role in determining its use for Scratching. When the closest trees (less than two metres) to the perimeter were distinguished from other more central trees, perimeter trees were Scratched to the same degree, whether considering any Scratching (χ^2= .0003, df= 1, p= .9857) or just the highest rates, "3" and "3+" (χ^2= .0003, df= 1, p= .9858). While the borders or perimeters of the areas were Scratched in the same proportions as the central region, Scratched trees were more densely located along heavily used pathways (χ^2= 44.518, df= 1, p<0.001), as were the more intensely Scratched trees, rated "3" and "3+" (χ^2= 30.001, df= 1, p<0.001). All cats, regardless of sex or age, contributed to the Scratch damage seen in the study.

4.7.3. FAECES

The use of faeces as a marker has been observed in many carnivore species (Gorman & Trowbridge 1989); in felids, it is less thoroughly documented, but deliberate defaecation may be the case in the Scottish wildcat (Corbett 1979), Spanish lynx (Robinson

& Delibes 1989), lynx, puma and bobcat (Macdonald 1985). However, the idea is not generally supported for domestic cats (Dards 1979), although faeces were seen deposited along well-used paths and in several middens (colloquially, a "dungheap" used by several individuals) in this and other studies (Corbett 1979; Fitzgerald & Karl 1979). In bobcats, middens are scattered throughout a range and are rarely re-marked (Macdonald 1980), so their presence may not indicate deliberate use of faecal markers, just as single conspicuous scats may be somewhat random; bobcat faeces are sometimes buried (Smith et al. 1989), which further brings their use as marks into question. Home-based cats have a tendency to cover or bury faeces, especially close to the core area (Liberg 1980; Panaman 1981), but may leave scats exposed, although not prominently displayed (Macdonald et al. 1987). There has been some suggestion that dominant and subordinate individuals differ, with dominants leaving more exposed scats (Macdonald 1980).

In total, the deposition of 55 scats was recorded in the present study, from November 1988 to March 1989. Adult Males contributed 16% of these, and Adult Females 71%, with the remainder from young non-Focal animals. Of these, a total of 27% were deposited within 10 metres of the central feeding area (33% of all Female faeces and 29% of Juveniles). All cats primarily defaecated outside a 10 metre radius of the food, and Males contributed 100% of their defaecations to this outer region. About one-third of all observed urine and faeces were left completely exposed, and the majority of these were not sniffed after deposition, for Males, Females and Juveniles (Table 4.12); in most cases a small attempt was made to scratch over the scats, leaving partially exposed results. Slightly more urine was deposited within the 10 metre radius, especially by Adult Females (45%); Males contributed 16% of all urine observed, and 66% was produced by the Females. Over all animals and including both urine and faeces, 70% of elimination occurred further than 10 metres from the food area.

It would appear that the cats in the study tended to urinate and defaecate away from the feeding areas, ultimately minimising contamination effects, especially important due to the prevalence of parasitic worms in the population. Cats showed a fairly strong inclination to leave faeces exposed, and locations included both conspicuous (along paths and in latrine areas) and inconspicuous sites. Faeces deposition was fairly obviously concentrated along the perimeters of the enclosures, perhaps corresponding to functional range borders. Males contributed significantly less observations, due to their reduced numbers, and so any conclusions are necessarily biased by the predominance of Females. Also, one Female suffered habitual diarrhoea, and skewed both total numbers and that of exposed scats. Unfortunately, the results are somewhat inconclusive for considering faeces as a useful marker; however, there is a hint that cats actively avoid feeding areas. With relatively limited space, elimination outside the core may necessitate some clumping of faeces nearer the perimeter.

Table 4.12: Elimination Patterns (Number of Observations from 25/10/88-23/3/89)

Category	Adult Males	Adult Females	Juveniles	All
Total Urine	7	29	8	44
Total Faeces	9	39	7	55
Sniffed	10	51	15	76
Exposed and Sniffed	0	4	0	4
Exposed, not Sniffed	6	17	0	23
Total Exposed	6	21	0	27
<10m from food	3	26	2	31
>10m from food	13	42	13	68
Urine, <10m	3	13	0	16
Urine, >10m	4	16	8	28
Faeces, <10m	0	13	2	15
Faeces, >10m	9	26	5	40

4.7.4. RUBBING ON OBJECTS

Cheek and Head Rubbing on objects was also considered a form of scent-marking in this study. Cats are widely described for their tendency to rub themselves on objects, other cats and people (Reiger 1979; Bateson & Turner 1988; Kerby & Macdonald 1988). As mentioned previously, large areas of a cat's body are richly supplied with glands that secrete fatty volatile substances; these regions include the thinly covered area anterior to the ears, the chin, lips and the base of the tail (McFarland 1987). These are the body parts used by cats when rubbing against animals or objects; rubbing on conspecifics was considered a form of social interaction and was included earlier in Chapter 4. Glandular secretions are richly scented, and probably vary with reproductive state and individual identity; saliva may also be involved (Ewer 1968; Reiger 1979). It is possible that secretions rubbed onto conspecifics are not marks, but act as a means by which the odours of known individuals are detected and become familiarised (Gorman & Trowbridge 1989; Smith et al. 1989). Females seem particularly interested in smelling skin gland secretion rather than urine marks (Verberne & De Boer 1976). Saliva, as transferred to the fur and paws during grooming, might also be a scented form of self-anointing, which reinforces individual identification (Gosling 1982). Reiger (1979) suggests that social carnivores (e.g. group-living) may scent rub more than solitary ones, which supports the contention that rubbing should be treated as a form of social interaction.

Overall, 240 Rubs were delivered during the present study, 193 of which were performed by Males (80%); when all individuals were considered, there was no significant difference between Males and Females ($U= 32$, $Z= -1.463$, $p= .144$, $n= 7,15$) and this was particularly the case for Juvenile Males and Females ($p= .902$). However, when Adults were compared, Males performed far more Rubs than Females ($U= 0$, $Z= -2.199$, $p<0.05$, $n= 2,11$). 64% of all Rubs were contributed by cats on Side B, but this was not significant over all cats ($U= 57.5$, $Z= -.167$, $p= .868$, $n= 10,12$), nor across Adults ($p= .347$) nor Juveniles ($p= .174$). The vast majority were evidenced by Adults, both Female and Male, but Juveniles played a small role, offering a total of 24 Rubs (10%).

The two predominant Adult Males were compared in terms of Rubs delivered, and Zac was found to Rub objects significantly more than Trossachs ($\chi^2= 32.667$, $df= 1$, $p<0.001$); this was an intriguing result in light of the fact that Trossachs was seen to Spray more often, and perhaps indicates the presence of alternative forms of Scent-Marking of objects. The composition of the odorous substances produced by such disparate organs is likely to influence aspects such as the longevity and potency of the marks; observers have noted the strong, pungent presence of spray, even for the

relatively insensitive human nose. Rub marks, however, have evoked little response or notice in researchers. A further possibility is that Spraying and Rubbing have distinctly different functions, and are therefore unrelated. Object Rubbing may also have simple grooming functions at times (e.g. the relieving of itches or removal of ectoparasites), but these are probably better performed through self-scratching, as part of grooming behaviour.

4.8. DISCUSSION

Many different aspects of behaviour have been examined in Chapter 4, linked by the common factor of specific behavioural observation, as opposed to Proximity (Chapter 3) or Reproductive details (Chapter 5). Three particular forms of data were presented: Focal observation, Occasional observation and Continuous observation (1987 only). Information was also subdivided by age and sex class, and into rare and common activities. Rare behaviour has been treated with a minimum of statistical analysis, due to the small sample sizes, while more common actions, because of their high frequency, were subject to more detailed tests. These included overall values, dyad measures, individual differences and seasonality. The form of analysis was dictated by the amount of data, and not by the type of behaviour, as it was uncertain as to which activities would prove more revealing.

One of the more commonly reported actions, that of tail-up behaviour (Dards 1979; Kerby 1987), was not noted in this study. In most cases, tail-up would have been included under the patterns Approach and often Follow and Rubbing. While presenting a strong indicator of intention, such that it appears to be involved in amicable "greeting" (Dards 1979), the absence of its measurement probably does not affect the conclusions which were made (especially as other elements of "greeting" were used - Close Sniff and Rubbing). Unlike Kerby (1987), while group behaviour rates may have differed, they were consistently correlated, showing a similar pattern over all activities. Weather variables were also found to have some linear relationship with certain actions, such as Following, Sniffing, Grooming and Rubbing. It is suggested that these effects resulted from differences in Female reproductive states, which tracked changes in daylength (van Aarde 1978; Follett 1985; Tabor 1989).

Adult Females appeared to be the basis for social organisation, in that they performed many actions which were unrelated to mere co-existence with others. The recipients of social interactions were not random, but involved specific partners for each

individual, as has been found with other studies on cats (Dards 1979; Kerby 1987). It was not evident that a social hierarchy was present, although some Females were more prone to initiation and others to receiving; the actual rank order was dependent on the particular activity, and it seemed more likely that individuals had different combinations of elements in their repertoires, and these lay along a continuum of intensity. Core members existed with each group, and these may correspond to the concept of Central Females, versus the less social Peripheral Females (Dards 1979; Kerby 1987). Unfortunately, groups were not numerous in size, and the enclosure too small, to fully consider this idea; more solitary cats could only get so far away, and this may merely have represented the variation possible within any core group. However, based on a synthesis of data and intuition, it is likely that, in the presence of open boundaries, the "anti-social" individuals would have moved further away from the rest of the group (rather than remaining) given the chance.

Females may behave socially to maintain the group, and thereby to ensure the group defence of resources against intruders and to facilitate the formation of maternal coalitions. The costs and benefits of such cooperative care are discussed more fully in Chapters 5 and 6. The presence of more intense (e.g. high interaction rates) relationships between cooperating Females than between less-involved cats may both reflect and presage the events of breeding. And events from any one year appeared to influence many subsequent situations, as seen from 1987 to 1988 and 1989 (e.g. Calico and Wanda, Becky and Poppy, Molly and Laura). The maintenance of amicable relations between certain dyads may enhance future opportunities for cooperation, assuming that cooperation yields net benefits.

Adult Males had two spheres of interest; the first was Females and access to mating opportunities. In this sense, Males also received attention from Females, some of whom initiated social acts to Males throughout the year (perhaps reflecting Male or Female preferences for a partner). The general subsets of behaviour involving the two sexes were concerned with mating, avoidance and minor agonistic conflict (Dards 1979; Kerby 1987). The second set of interactions involved other Males; Male-Male actions were almost all aggressive (Corbett 1979; Dards 1979), and doubtless reflected the selection on Adult Males to maintain their access to Females and other resources (all limited by the fences around the enclosures). Females, Juveniles and Kittens behaved at times in ways which might have diminished levels of Male agonism towards them; Rolling might play some role to this end, acting as a form of submission similar to that in canids (Fox 1975a; Huntingford & Turner 1987), and used by Juveniles to Adult Females as well as to Adult Males. Males did little that indicated a role in the maintenance of group structure and social bonds, which supports the observations of Males as more solitary individuals who visit Female groups for mating purposes.

Juveniles behaved like less social Adults for the most part, perhaps reflecting the period of observation, which straddled their maturation to Adulthood. Females were again more involved in contact activities, especially toward familiar Adult Females, and during late Gestation and Breeding. Males tended to remain apart in small Juvenile groups, as in Kerby (1987), perhaps avoiding the aggression of the resident Adult Male (and Adult Females); these young Males were sufficiently covert as to have far fewer observations due to reduced availability, and rarely came into the open when the Adult Male was visible. Young Males later dispersed upon reaching full maturity, and seemed little concerned with group bonds. Overall, it would appear that, despite varying intensities of actions, Juvenile Females behaved in a way that could help the formation of amicable relationships, while Males lacked these more bonding overtures and were more wary of contact and other cats. Carbonel was the notable exception and made repeated Rubs, especially when younger, to Adult Females; perhaps related to this was the fact that Carbonel had the fewest Fights with the resident Adult Male (n=1) and typically only Mounted immature Females.

Adult Females focussed first on Juveniles when young (e.g. Kittens) and then again later when they reached maturity, and relatedness appeared to have some influence; mothers and sons or daughters were more mutually interactive than others, as were allomothers or close helpers with younger cats. This probably reflects the proposed matrilineal basis for groups, although it was surprising that Females maintained relatively close relationships with sons destined for dispersal; perhaps this is one way of socialising Males for their interactions with other Females, or helps to reduce Male aggression to subsequent litters born to their mothers. How is it possible to explain the strong helping role by Males to Calico's kittens? Generally, it appeared that early amicable experiences may lead to later reinforcement of these relationships by the Juvenile (also in primates: Berman 1983a), as evidenced by the positive interactions with mothers, allomothers and "aunts". This can then be interwoven with other aspects, such as inter-Male agonism, and the specifics of an individual's later encounters.

Kittens mainly interacted with Females; Males showed some variation in their tolerance for Kittens, ranging from Trossachs, who avoided them completely and with vigour, to Catkin and Zac, who occasionally Groomed and Rested with Kittens (as in Dards 1979); Males also showed passing interest in Mounting Kittens, as seen by Kerby (1987). Females performed all the usual maternal tasks, including Nursing, Grooming and Playing. As Kittens aged, they began to resemble Juveniles more in behaviour, and were considered as such after the end of their birth year. Retrieval behaviour seemed to be more prevalent in the reproductively experienced Females; Wanda spent a season as a nulliparous

allomother, unlike her inexperienced primiparous counterparts, and was observed to perform more retrievals than other primiparous individuals. There is no indication that retrieval enhances Kitten survival, but this is a possible consideration for free-living cats with more predation pressure or more hazardous nest sites. Other aspects of maternal-type behaviour are discussed in Chapter 5.

Scent-Marking was also examined. Females were rarely seen to Spray (also in Macdonald & Apps 1978; Dards 1979; Kerby & Macdonald 1988), but they Rubbed objects more than did Males. Urine-Spraying showed some seasonal patterning, suggesting a link with reproductive states. Adult Males differed in their rates of Spraying and object Rubbing; it is possible that this variation reflected either differences in "status" or "territoriality". Adults were found to Rub more than Juveniles, and Males Rubbed more than Females, perhaps supporting the concept of Rub-Marks as territorial (or status) indicators. Occasionally, cats were seen to Spray an object after Rubbing on it (Corbett 1979; Dards 1979; Panaman 1981), but never in the reverse order. Trees along paths were Scratched more than trees along the perimeter or in the general area of each side of the enclosure and held little support for the concept of a territory defined along its perimeters (as with Sprays in Panaman 1981). Trees with species-specific soft bark were Scratched more than hard-barked trees. Cats mainly eliminated away (greater than 10 metres) from the feeding area. Faeces were often left exposed (Corbett 1979; Liberg 1980; Panaman 1981); cats often left these deposits without sniffing them (Macdonald et al. 1987), as has been suggested for the idea of faeces as territorial markers, but no clear pattern was discernible in this study. In addition, some faeces were arranged in apparent "middens". The results of this scent-marking data are discussed at greater length in Chapter 6.

Once the basic social structure of this particular population was established from the Focal behaviour data (building on top of the spatial relationships seen in Chapter 3), a more specific investigation was undertaken. The remainder of the chapter asked the following questions: "could social relationships be predicted from one season to the next?", "were cooperative partners distinguishable before the birth of litters?", and "were Solitary and Communal Females distinguishable outside the breeding season?"

Focal data were divided into seasonal subgroups to further elucidate the influence of breeding relationships (Male-Female mating and Female-Female cooperation) on year-long interactions. Monthly differences reinforced the idea of reproductive influences, such that mating-type actions were predominant in early months, while contact activities were spread over the year depending on the details of individuals and behaviour. Behaviour by breeding Females showed consistency throughout the year in terms of the

more general Follow and Approach, as well as Close Sniff; these investigative and reinforcing actions were constantly maintained. Evade and Swipe were related from Winter through Gestation to Breeding, with no carryover to later seasons; as these activities mainly concerned Males and less social Females, it is not unlikely that breeders continue to ward off others from their litters, as well as maintaining agonistic relations through non-breeding times of the year.

Contact-related actions were more peripatetic; Rubbing rates were associated from season to season, and year to year (Both Gestation and Breeding). Females returned to the same partners at similar levels throughout the year; and associations from one Breeding to the next were not merely the product of year-round levels, as 1989 Breeding lacked a strong connection to the previous several seasons, while resembling the past year. Grooming rates were strongly related to actions over the previous Winter, as was Resting in its links between Winter and Gestation (the colder months usually).

As for actions by other cats to breeding Females, these showed different sets of associations. Follow, Approach and Close Sniff were similar to the Female-initiated pattern, and were, if anything, more consistent from one season to the next, with fewer cross-links; late summer breeding appeared as a bit of a behavioural anomaly, and rates were rarely connected, except to the subsequent Winter (whereas for Females, there were associations between different Breeding seasons for Approach). Evading of Females showed little relation from one period to another, except perhaps in 1989 between Gestation and Breeding. Social Rubs were more general, and showed strong associations from Breeding to Winter and Winter to Gestation; they may be more common just before, and not during, cooperative efforts, when much time is spent Resting in Contact and out of view. Grooming and Swiping were related between Gestation periods, while Resting showed associations between colder seasons (Winter and Gestation) as well as between Breeding periods in the same year (1988).

When breeding Females and their helpers and partners were singled out, a slightly different pattern was seen. Follow, Close Sniff, Swipe and Groom were consistent year-round; Approach linked Winter with Gestation_1 and Breeding_1; Body Rub and Rest in Contact were related from Gestation to Breeding, and across the two years; and Evade was similarly low for Breeding_1 in 1988 and 1989. Unfortunately, the behaviour tested in this way was limited to more common, but perhaps less relevant, actions; but there are indications that cooperating Females reinforce amicable alliances all throughout the year, heighten Approaches, Rubs and contact with one another preceding the birth of Kittens, and minimise evasion tactics. Grooming and Resting together may originate during one Breeding, resume during the huddling of early Gestation, and be repeated in subsequent Breeding periods, when cooperative alliances are re-ignited.

One problem with the interpretation of these results was the dissimilar breeding patterns among Females, such that only some had second litters in the year; therefore $Breeding_2$ was a subset of the Winter as defined for other Females. Gestation and Winter doubtless overlapped slightly due to the assumption of a constant gestation length. Also, the previous Winter (1987-88) and following Breeding (1989) would have offered still more information had they been completely sampled. And the additional confounding factor was the inclusion of Females from both groups; numbers would have been too small and meaningless otherwise, but as discussed earlier, the two groups did show some behavioural differences overall, dependant upon the individuals making up the membership of each group.

A second problem concerned the data for later breeding attempts, affecting the periods $Gestation_2$ and $Breeding_2$. As most of the second (and third) litters failed soon after birth, the time representing these seasonal periods is often curtailed and confined to a few days. The relative infrequency of many social interactions may have meant that the sample time was too short to get a full view of interactions; therefore, with more samples and longer second Breeding seasons, these later periods might have fit the yearly cycle. Other possible reasons for the lack of correlations with other reproductive seasons include the lack of breeding synchrony for later litters (allowing only cooperation from helpers, but not full communal care) or a carryover effect from the last season, such that many mothers were still caring for maturing kittens (and often engaged in other cooperative alliances).

Generally, the pattern that emerged was similar to that seen in spatial relationships described in Chapter 3. Behaviour that could be interpreted as being concerned with more general categories, such as Approach and Follow (which could be part of contact, agonism, mating or other advances), were less well defined; these activities took place at similar levels throughout the year, perhaps for differing reasons with changing reproductive state, although the data could not resolve such detail. With more specific behaviour, those actions with apparent social contexts such as agonism and affiliation, a cycle was again discernible. Winter, spring Gestation, spring Breeding, and again Winter seemed the basic pattern, with little connection to any second or third reproductive attempts in a year (although this was not necessarily indicative of a separation of relationships, as discussed above).

Spring Gestation periods often showed related levels of behaviour between certain dyads, as occasionally did spring Breeding periods. Cats who shared some effort in cooperative reproductive attempts had particularly strong recurring associations. Perhaps Females sought out the same partners in subsequent years, based on experience; the links seen with future helpers and partners may presage and form the basis for cooperation. The continuance of amicable interactions through Breeding and into the following Winter may facilitate stability in relationships. The lack of interconnections

between random periods suggests that the cycle of associated seasons is a real effect, and that there is a predictive element to seasonal behaviour which may have a substantial influence on reproduction and cooperation.

Therefore, in answer to those questions posed earlier in the discussion, it would seem that social relationships can be predicted from season to season (based on the reproductive states of Females) and from year to year, especially for affiliative activities. Cooperative partners could be detected before the start of the relevant Breeding period, and showed particularly consistent interaction levels throughout the year. Communal Females showed more associations between affiliative social relationships over the various reproductive seasons, while Solitary Females were less consistent (and often had fewer interactions, especially those of an amicable nature). The component aspects of reproductive attempts and the presence of several styles of care, Solitary and Communal, are explored in Chapter 5. The final discussion, integrating the results of the analyses of spatial relationships (see Chapter 3), social relationships (this chapter) and reproductive associations (see Chapter 5), is presented in Chapter 6, placing the findings of this study into a broader theoretical perspective.

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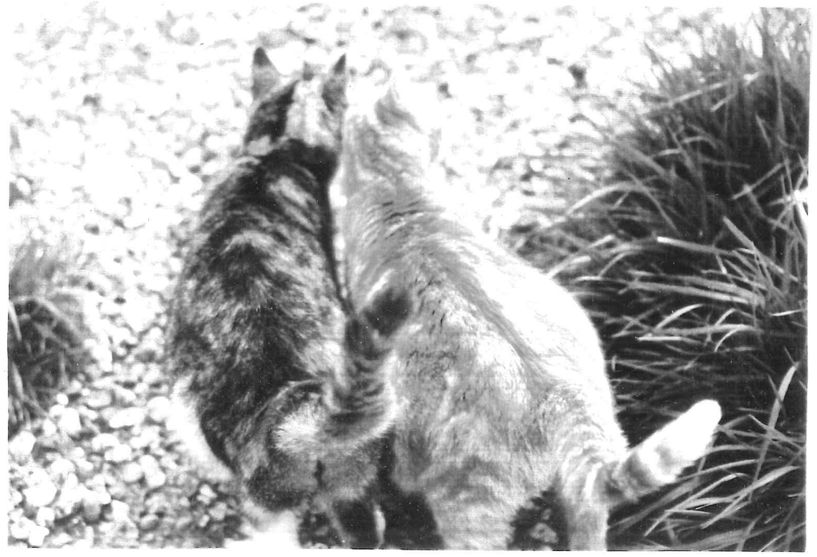
An adult female, Wanda, suckling her own kitten (back) and an older kitten, Camille (front). Wanda's kitten is 8.5 weeks old, and Camille is 14.5 weeks old. Wanda was an allomother to Camille and her littermates (n=4) prior to and following the birth of her own litter (n=4). (see Section 5.5.5)

Two adult females, Poppy (left) and Tessa (right) nursing the kittens of a third mother, Becky. (see Section 5.5.5 and Chapter 6)

Two pregnant adult females, Becky (left) and Tessa (right) head rubbing (and later body rubbing). Tessa later helped (and suckled, as above) Becky's litter after the death of her own kittens. (see Section 5.5.5 and Chapter 6)



Chapter 5

Maternal Behaviour

5.1. GENERAL INTRODUCTION

5.1.1. PREFACE

Domestic cats are semi-altricial mammals, and give birth to offspring which are completely dependent upon parental care for early survival. In the absence of active male parental care, the burden of rearing offspring to the age of independence falls to the mothers (see Section 1.3.2).

As with all animals, the maximisation of the number of offspring raised successfully to independence is taken as a measure of individual fitness, through the consideration of reproductive success (Brown 1988; Clutton-Brock 1988); individuals are adapted, through natural selection over the course of evolution, to optimise fitness through behaviour which enhances offspring survival. Therefore, differences in the maternal behaviour of cats may lead to differences in the mortality rate of kittens.

This chapter investigates four possible sources of variation between females and their effects on offspring survival and other measures of maternal care. The first section examines differences between the two groups in the study, to investigate the possibility of inter-group variation prior to pooling the available females. The second section compares Primiparous females with Multiparous females to look for any effects of reproductive experience on care and mortality. The third section distinguishes between females partaking of two different maternal styles, Solitary and Communal care, and examines the differences between these types of care and the females involved. The fourth main section deals with the question of individual variation, particularly in the area of reproduction, and asks whether individuals vary too greatly for consideration of broader categories. Later sections briefly explore females for differences in kitten development (Section 5.6), as well as looking at a measure of reproductive success (Section 5.7), the sources of kitten mortality (Section 5.8), and aspects of nest site variation not included in previous investigations (Section 5.9). As with previous chapters, Figure 2.2 should be used to identify the specific individuals mentioned in the following sections.

5.1.2. COLLECTION OF DATA

A number of variables were noted for the analysis of maternal reproduction (Table 2.4). These ranged from recordings of Date of Birth, Mother's Age and Parity, Littersize and Type of Care (all concrete aspects), to considerations such as Maternal Time Budget (defined in Section 2.4.4.1), Kitten Mortality and the number of Nest Sites in which litters were raised. Over the first six weeks following the birth of a litter, mother

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and kittens were focally observed for two hours each day, and any changes, such as the death of a kitten or presence of a new helper, were recorded. This yielded a set of variables for each mother and each litter.

Unfortunately, due to the secluded nature of nest sites and the mothers' penchant for privacy, it was often impossible to see into nests until several days after birth. As a result, actual Littersize-at-Birth is not known for some of the cases. Several authors (Kerby 1987; Bekoff 1989) have noted the problem associated with the estimation of littersize in the field; factors such as the pooling of litters, early mortality and sporadic absences (of kittens and mothers) from the den exacerbate the difficulty. More importantly, when several pregnant females disappeared together, only to emerge from a shared nest after parturition, it was impossible to ascribe a specific Littersize to each female and to assign known maternity to any single kitten. The instances where this was a problem were few, but became most prominent in 1989. Littersize was estimated from all known littersizes born to that mother; maternal identity was more problematic. Coat colours provided some clues as to maternity, especially in the cases of ginger females and kittens, but they were not sufficient.

With an estimated number of kittens (based on the sizes of each mother's previous litters), two mothers (or more) were allocated the kittens most likely to be related by coloration, then assigned any others at random. Judging from the observation that completely communal litters of this sort appeared to be suckled indiscriminately, and the fact that mortality was low for those litters concerned, it matters little which specific kitten matched with which mother. This limitation mainly affects the analysis in Section 5.7 on Reproductive Success; the justification behind each decision regarding maternity is strong enough to state results with a large degree of confidence. Only genetic fingerprinting would have ascertained the definite maternity of each kitten, and this was unfortunately not possible without a Home Office licence (not necessary for the rest of the study).

5.1.3. DATA ANALYSIS

All females and litters were used for the analysis of certain reproductive aspects: Date of Birth, Parity, Littersize-at-Birth (when known) and Mother Age. However, there were a number of litters which were classed as being "non-viable"; in such cases, the mother usually failed to provide any maternal care and the litter suffered complete mortality within 48 hours of birth. In several instances, entire litters of neonates disappeared without a trace. These "non-viable" litters were removed from the data set when considering Time Budgets and Nest Sites.

All variables were tested for normality, using both graphical and statistical methods. Although kurtosis and skewness were often within normal bounds, histograms

showed enormous deviation from a normal distribution. Each variable was subjected to a range of transformations (Martin & Bateson 1986), but it was not possible to normalise the majority of them. Those that did transform successfully to normal distributions (6 out of 20) were tested using both parametric and non-parametric statistics; there were no differences in the outcome of the tests, so it was decided to use non-parametric tests for the entire data set, as most variables were non-normal. Non-parametrics allowed the comparison of otherwise incompatible variables, and the data were left untransformed. In addition, non-parametric tests are more robust, and any significant results are likely to be true (fewer Type I errors) due to the slightly reduced power compared with the equivalent parametric statistics (Martin & Bateson 1986).

All reproductive factors were tested using a Kruskal-Wallis test in place of the parametric Analysis of Variance (ANOVA) method. The "Within Individual Female" variation proved to be as large as, or greater than, the "Between Individual Female" variation for all variables (e.g. a small H-score with an attendant non-significant probability value; Table 5.1). These scores were then double-checked by looking at the variances (sums of squares), and the same conclusion was reached (e.g. the variation within individuals was greater than the variation between individuals). As a result, most statistical comparisons were made using each litter as a separate datum point; these data were not considered to be subject to the problems of the "pooling fallacy" (Machlis et al. 1985), since litters were treated as a unit (as opposed to their constituent kittens) and the high degree of variation between individual litters suggested that the maternal effect was much smaller than other effects; the data were thus shown to be independent. Only the differences between Mothers were tested with means over all litters for each variable, as these would be drastically affected by the high degree of intra-individual variation.

The non-parametric statistical tests used to analyse the reproduction data included the Mann-Whitney U-test to compare two samples, with a correction factor for tied values, the Kruskal-Wallis test, a one-way analysis of variance by rank for three or more groups, also weighted by a correction factor for tied scores, the Spearman Rank Correlation Coefficient, with a correction for ties, and χ^2 tests (based on a 2x2 contingency table with a Yates correction). All tests were two-tailed and used a significance level of α=0.05. (Sokal & Rohlf 1981; Zar 1984) Non-significant probability levels are quoted to two significant figures, in keeping with the small sample sizes.

Table 5.1: Results of Kruskal-Wallis Tests for Independence of Data. Non-significant probability levels indicate that the within-female variation is as great or greater than the between-female variation. As a result, each litter, regardless of mother, was used as a separate datum for subsequent analyses.

Variable		df	n	H	p
Date of Birth		13	37	6.330	.93
Littersize-at-Birth		13	33	12.816	.46
Littersize		13	37	12.910	.45
Communal Littersize		13	39	12.425	.49
Time Budget:	Week 1	13	39	14.136	.36
	Week 2	13	38	14.276	.35
	Week 3	13	38	16.181	.24
	Week 4	13	37	15.319	.29
	Week 5	13	38	15.325	.29
	Week 6	12	37	14.897	.25
	Weeks 1-3	13	38	13.871	.38
	Weeks 1-6	13	36	12.906	.46
Mortality:	Weeks 1-3	12	31	13.155	.36†
	Weeks 1-6	12	31	14.777	.25†
	To 4 Months	7	24	5.047	.65†
Nest Sites:	Weeks 1-3	7	18	10.518	.16
	Weeks 4-6	7	15	11.196	.13
	Total	7	15	10.961	.14

(N.B. Both Parity and Mother Age showed significant differences between females, due to the presence of young primiparous females. Excluding the four primiparous females from 1987 and 1988, the remaining females showed larger differences within individuals)

† Jenny was not included in these statistics as all her litters failed and she was generally removed from the mortality analysis throughout the chapter, except where noted specifically.

5.2. GROUP DIFFERENCES: Side A versus Side B

5.2.1. DATE OF BIRTH

When all females and all litters were considered, the two groups did not differ in regard to Date of Birth of litters (Mann-Whitney: U= 167, Z= -0.122, p= .90, n= 18,19; Figure 5.1.a). There was a noticeably high degree of sychronisation in both oestrus and parturition, especially in 1987 and 1989. The females tended to have one or two litters per year, adhering to a seasonal pattern as commonly described for feral cats (Ewer 1973; Corbett 1979; Liberg 1981). Litters were clumped in the spring months, late March to May, with a secondary birth peak around June to August (Figure 5.1.b). An occasional litter was born later in the year, but these were invariably unsuccessful. The most extreme case was a litter born to Poppy (Side A) in early December; despite the mother's attempts to rear the litter in the winter cold, the last kitten died (potentially of exposure) just as it reached the end of its first 6 weeks.

Females from both groups were pooled for all subsequent analyses of Date of Birth (see Sections 5.3.1 and 5.4.1).

5.2.2. LITTERSIZE

The Littersize-at-Birth, or total number of kittens born in each litter to each mother, did not show any significant difference between the two groups (U= 129, Z= -0.257, p= .80, n= 17,16; Figure 5.2.a). The groups produced, on average, similarly-sized litters. It was not possible to include Littersize-at-Birth for all litters, as some of them disappeared soon after birth. In most cases, the number should be accurate; kitten remains were included in the estimate, but there is a slight possibility that a few kittens were completely consumed before a count was made. This measure was considered to be relatively accurate.

A second littersize measure was also used, called simply "Littersize". It refers to the actual number of kittens raised in each litter. In effect, it is equal to the Littersize-at-Birth minus any kittens stillborn or cannibalised at birth. Upon occasion, a litter would show attrition in numbers through the first few weeks, but this was rare; the Littersize accounted for the number of kittens in which a mother had to invest for most (if not all) of the 6-week focal period. Again, the size of litters raised, as measured by Littersize, showed no difference between the two groups (U= 128, Z= -1.328, p= .18, n= 18,19), when all litters were included (Figure 5.2.b). If only viable litters (i.e. those which survived the first few days and therefore not including any instances with Littersize=0, which obviously required no maternal reproductive effort past parturition)

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5.2.2. LITTERSIZE

The Littersize-at-Birth, or total number of kittens born in each litter to each mother, did not show any significant difference between the two groups (U= 129, Z= -0.257, p= .80, n= 17,16; Figure 5.2.a). The groups produced, on average, similarly-sized litters. It was not possible to include Littersize-at-Birth for all litters, as some of them disappeared soon after birth. In most cases, the number should be accurate; kitten remains were included in the estimate, but there is a slight possibility that a few kittens were completely consumed before a count was made. This measure was considered to be relatively accurate.

A second littersize measure was also used, called simply "Littersize". It refers to the actual number of kittens raised in each litter. In effect, it is equal to the Littersize-at-Birth minus any kittens stillborn or cannibalised at birth. Upon occasion, a litter would show attrition in numbers through the first few weeks, but this was rare; the Littersize accounted for the number of kittens in which a mother had to invest for most (if not all) of the 6-week focal period. Again, the size of litters raised, as measured by Littersize, showed no difference between the two groups (U= 128, Z= -1.328, p= .18, n= 18,19), when all litters were included (Figure 5.2.b). If only viable litters (i.e. those which survived the first few days and therefore not including any instances with Littersize=0, which obviously required no maternal reproductive effort past parturition)

Figure 5.1.a

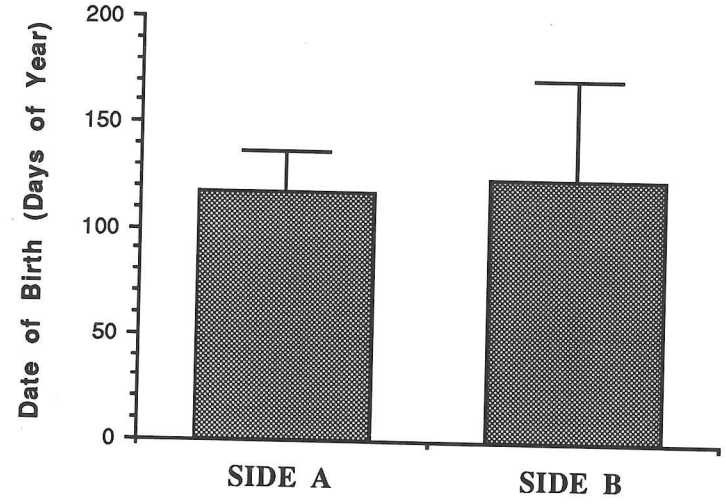

Figure 5.1.b

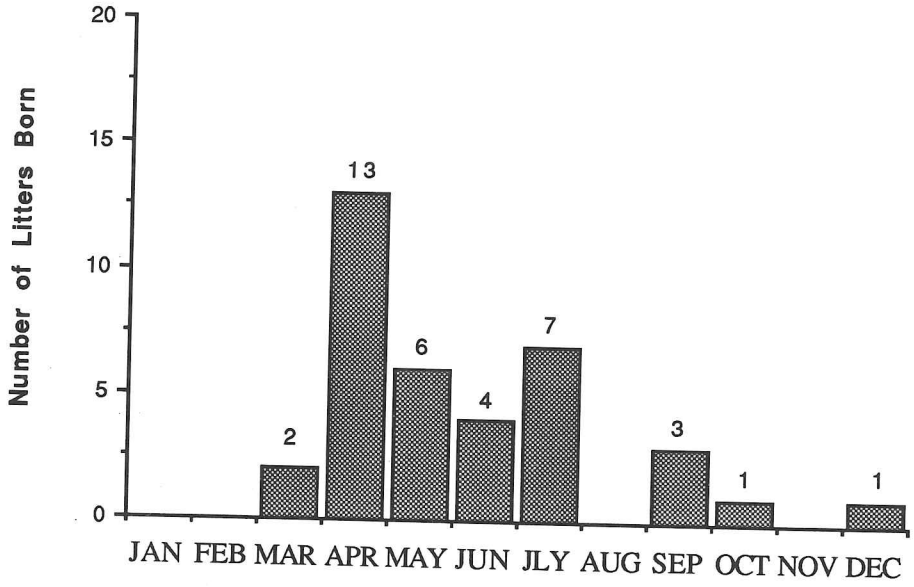

Figure 5.1: The Date of Birth of litters. (**a**) Differences between the two Female groups in Sides A and B (medians and interquartile ranges are given); (**b**) The timing of all litter births for each month (over all three study years).

Figure 5.2.a

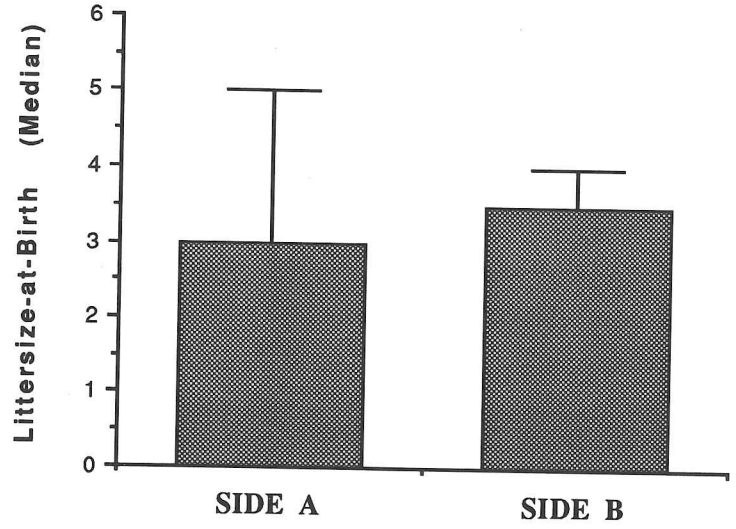

Figure 5.2.b

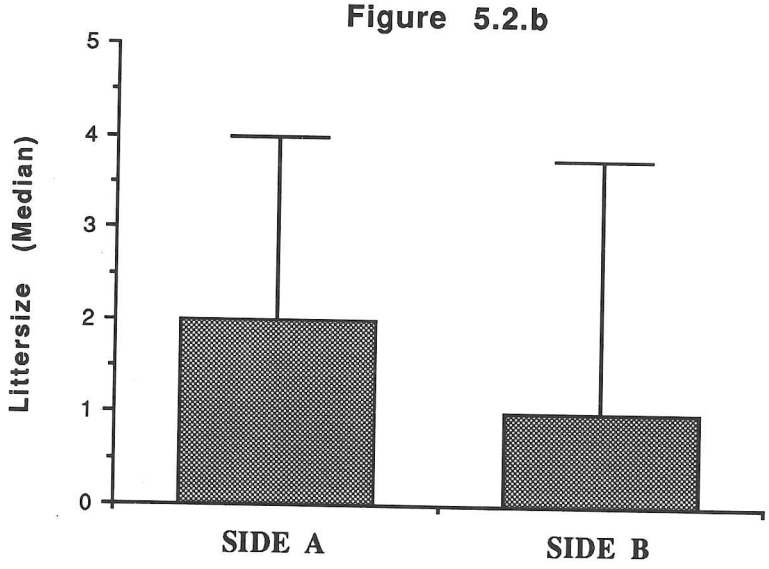

Figure 5.2: Littersize measures for the two groups of cats, Sides A and B. Medians and interquartile ranges are given. The differences between the groups were not significant using Mann-Whitney U-tests. (a) Littersize-at-Birth; (b) Littersize (equal to the Littersize-at-Birth minus stillborn kittens and any kittens that died within the first two to three days after birth).

were considered, the difference between groups was still non-significant (U= 62.5, Z= -0.22, p= .83, n= 12,11).

As with Date of Birth, Littersize-at-Birth and Littersize were pooled for all females in both groups in subsequent analyses (see Sections 5.3.2 and 5.4.2).

A third littersize measure was calculated, the Communal Littersize. This accounted for the combination of litters by two or more females such that Communal Littersize= Σ (Littersize of Female$_i$). When the two female groups (Sides A and B) were compared over each female, Communal Littersize differed significantly (U= 103, Z= -2.47, $p<0.05$, n= 18,19). Side A females had larger communal litters, probably due to the presence of Becky, who was always communal and who tended to have large litters (mode=6). This analysis is based on the Communal Littersize for each female and each litter; when just the litters themselves are included, and not duplicated for each contributing mother, the inter-group difference disappears (U= 62.5, Z= -1.488, p= .14, n= 11,16), such that, overall, communal litters were of similar size in the two groups.

5.2.3. MATERNAL TIME BUDGET

Considering only those mothers that actively reared kittens (e.g. excluding the cases where litters failed within several days of birth due to apparent lack of maternal care), females on Side A and Side B did not differ in Maternal Time Budget (Figure 5.3.a). This held for weekly comparisons (Week 1: U= 49, Z= -1.047, p= .30, n= 12,11; Week 2: U= 60, Z= -.033, p= .97, n= 11,11; Week 3: U= 37, Z= -1.543, p= .12, n= 11,11; Week 4: U= 40.5, Z= -1.021, p= .31, n= 11,10; Week 5: U= 41, Z= -1.253, p= .21, n= 12,10; Week 6: U= 37, Z= -1.268, p= .20, n= 11,10) and comparisons over longer periods (First three weeks: U= 45, Z= -1.018, p= .31, n= 11,11; All six weeks: U= 44, Z= -.454, p= .65, n= 10,10; Figure 5.3.b). All females and litters were subsequently pooled for analyses of Maternal Time Budget (see Sections 5.3.3 and 5.4.3).

5.2.4. KITTEN MORTALITY

If all litters are considered, the two groups of females did not differ significantly on the number of kittens that died within any of the three specified time scales (Figure 5.4): Weeks 1 to 3 (U= 147.5, Z= -.753, p= .45, n= 18,19), Weeks 1 to 6 (U= 151, Z= -.643, p= .52, n= 18,19) or over the first four months (U= 109, Z= -.068, p= .95, n= 13,17). This analysis includes those litters which were abandoned or neglected within hours of birth. If only "viable" litters are included, those which received maternal care and attention from birth, the results remain unchanged over the three mortality periods.

Figure 5.3.a

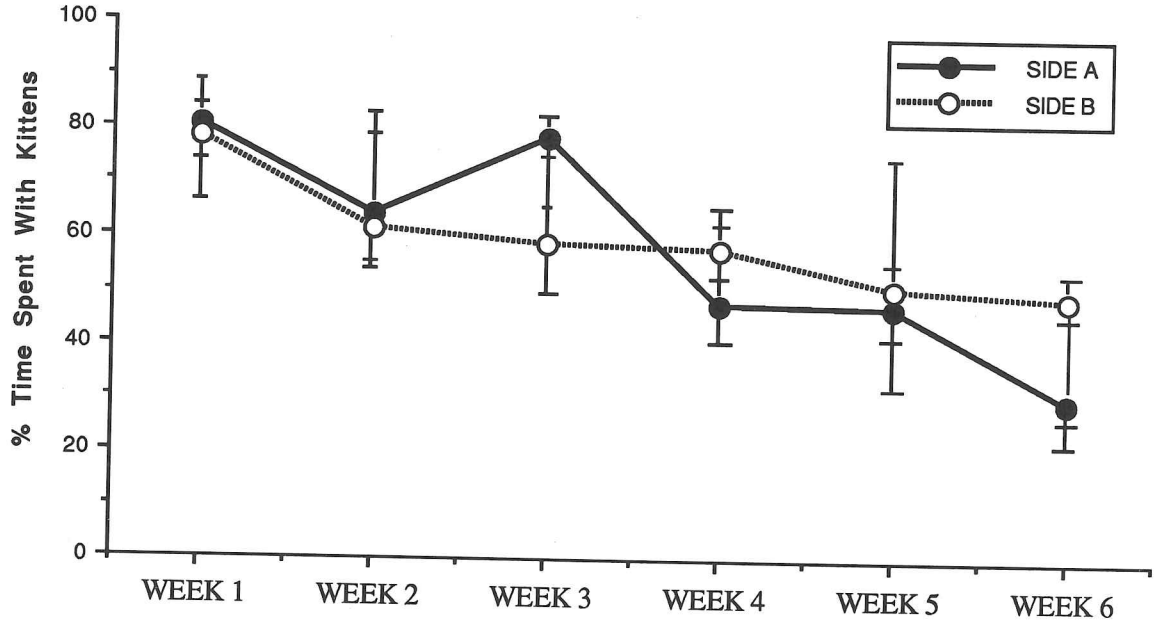

Figure 5.3.b

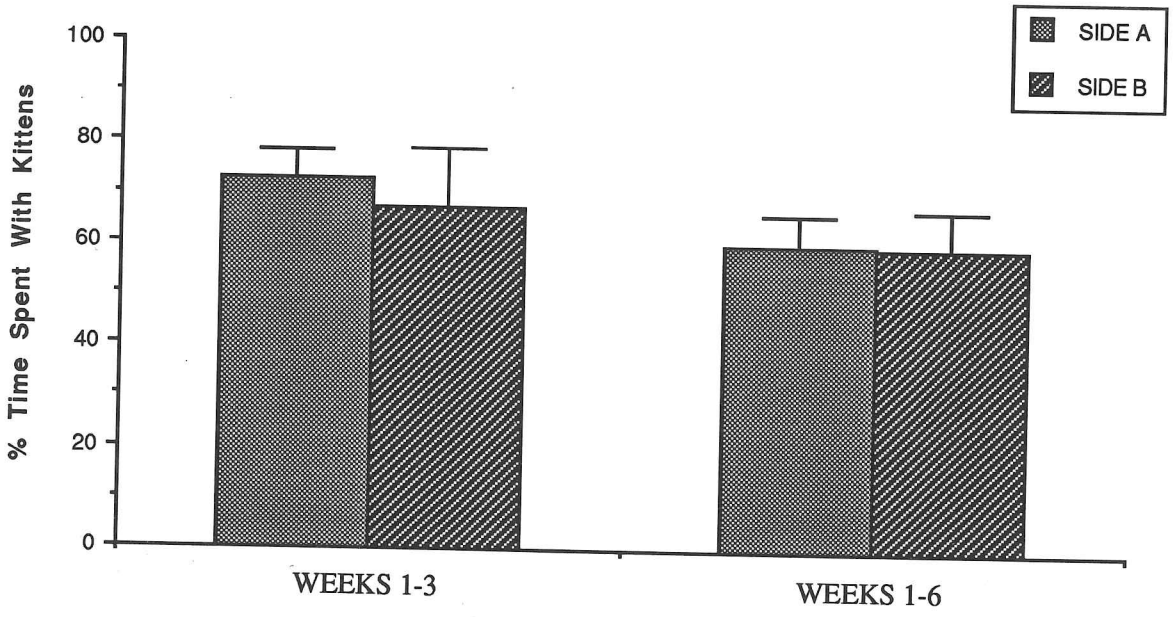

Figure 5.3: Maternal Time Budget comparisons between the two groups. The differences between the groups were non-significant with Mann-Whitney U-tests. Medians and interquartile ranges are shown. (**a**) Each of the first six weeks after birth; (**b**) Lumped sums for the first three weeks (Weeks 1 to 3) and all six weeks (Weeks 1 to 6).

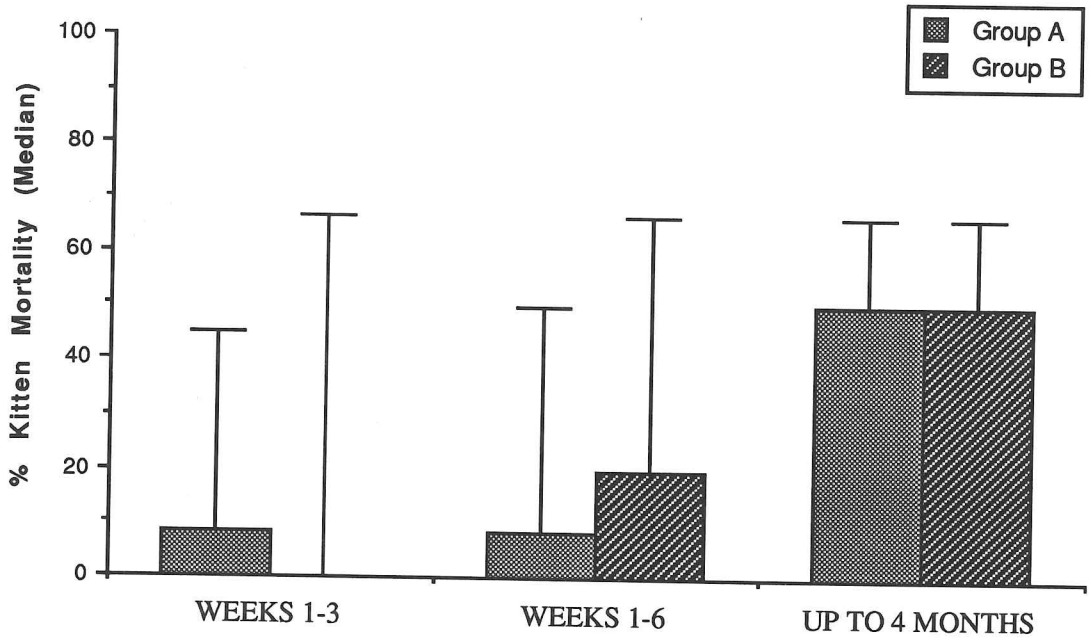

Figure 5.4: A comparison of the Kitten Mortality rates between the two groups. These were found for three different time periods, the first three weeks after birth (Weeks 1 to 3), the first six weeks after birth (Weeks 1 to 6), and the first four months after birth (Up to 4 Months). Values were calculated as the proportion of kittens per litter that died within each time period. The differences were non-significant between the two groups using Mann-Whitney U-tests. Medians and interquartile ranges are shown. Where the median was zero, interquartile ranges stem from the x-axis.

Females from Sides A and B were pooled for proceeding comparisons (see Sections 5.3.4 and 5.4.4).

5.2.5. NEST SITES

Females used a variety of locations as sites in which to raise kittens. The number of Nest Sites tended to vary, from as few as one over the first three weeks to as many as eleven over all six weeks. Groups did not differ in the number of Nest Sites used over all six weeks ($U= 30$, $Z= -1.525$, $p= .13$, $n= 10,10$). However, females in Side A used a significantly greater number of Nests over the first three weeks ($U= 25$, $Z= -2.582$, $p<0.01$, $n= 12,11$), although the discrepancy disappeared for the last three weeks ($U= 47.5$, $Z= -.194$, $p= .85$, $n= 10,10$)(Figure 5.5). As will be seen in Section 5.4.5., this difference is undoubtedly due to a difference in the distribution of maternal styles between the two sides. Nest Sites, over each time period, were pooled for considerations of Parity, and will be investigated later in the chapter (see Section 5.4.5).

5.2.6. OTHER VARIABLES

The two groups, Sides A and B, displayed no significant difference in regard to Parity ($U= 140$, $Z= -.952$, $p= .34$, $n= 18,19$) or the related variable, Mother Age ($U= 119$, $Z= -1.58$, $p= .11$, $n= 18,19$). Mothers were similarly distributed, such that both groups had younger and older mothers as well as primiparous and multiparous females.

5.3. EFFECTS OF PARITY: Primiparas versus Multiparas

5.3.1. DATE OF BIRTH

Primiparous mothers were primarily those females born into the colony in 1987 and 1988, who survived to breed in 1989; the numbers were supplemented by several of the founding adult females, who bred for the first time in 1987 or 1988. As expected, Primiparous and Multiparous mothers showed a substantial difference in Maternal Age ($U= 1$, $Z= -4.033$, $p<0.001$, $n= 7,30$; Figure 5.6.a), with a median age of 1.79 years in Primiparas compared to 5 years for Multiparas. Despite the disparity in age and maternal experience, Date of Birth did not differ between the two groups ($U= 69$, $Z= -1.397$, $p= .16$, $n= 7,30$; Figure 5.6.b). Females, regardless of the influence of age or experience, tended to fall into a reproductive timing synchrony, both of oestrus (mainly estimated by birth date and casual behavioural aspects such as lordosis) and of parturition.

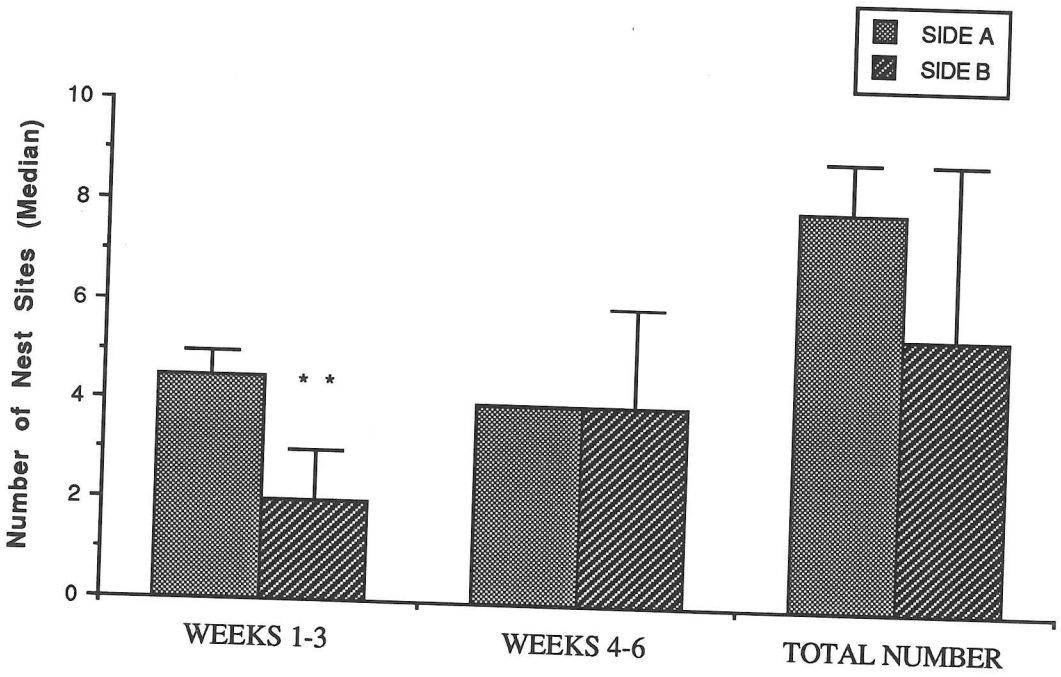

Figure 5.5: The number of Nest Sites used by Females in the two groups. Medians and interquartile ranges are shown. The third interquartile range was the same as the median for Side A in Weeks 4 to 6, hence the absence of a range marker. **$p<0.01$, Mann-Whitney U-test.

Figure 5.6.a

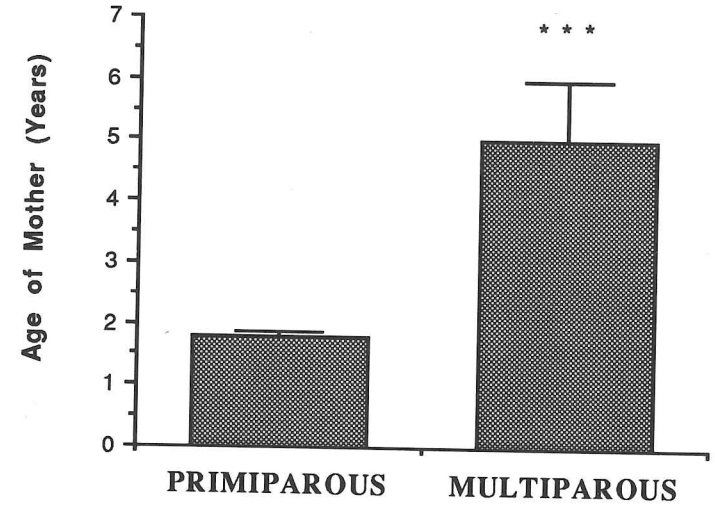

Figure 5.6.b

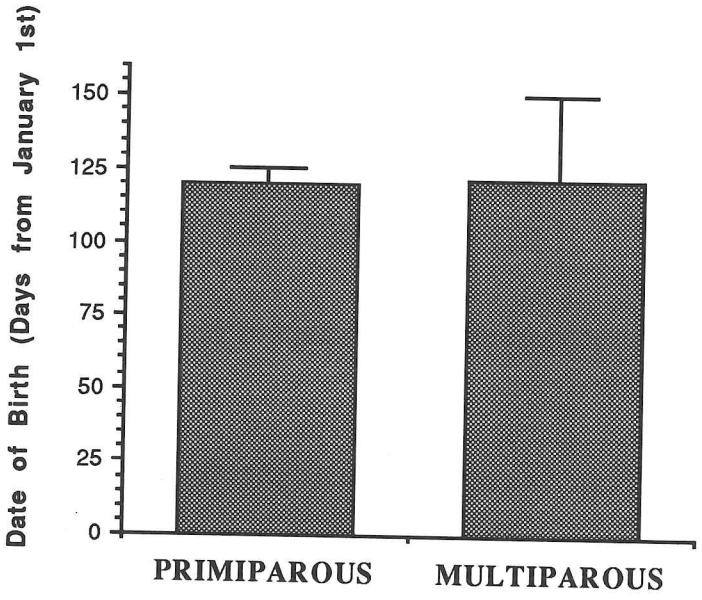

Figure 5.6: Differences between Primiparous and Multiparous mothers. Medians and interquartile ranges are given. (**a**) Maternal Age; (**b**) Date of Birth of first litters (of the year). ***p<0.001, Mann-Whitney U-test

5.3.2. LITTERSIZE

Primiparous females tended to give birth to small litters (median=2) compared to the more experienced females (median=4); the Littersize-at-Birth was significantly larger for the Multiparas ($U= 41.5$, $Z= -2.218$, $p<0.05$, $n= 7,26$; Figure 5.7.a). However, due to the presence of stillborn kittens, and the possibility of neonatal mortality and cannibalism, the size of the litters which were actually reared (and not just birthed) did not differ ($U= 101$, $Z= -.158$, $p= .87$, $n= 7,30$; Figure 5.7.b).

Communal Littersize did not differ significantly between Primiparous and Multiparous females, whether calculated from each female and each litter ($U= 96$, $Z= -.353$, $p= .72$, $n= 7, 30$), or from the vantage of each Communal litter (without inclusion of a value per contributing mother) ($U= 36.5$, $Z= -.771$, $p= .44$, $n= 4,24$). This is likely to be a logical outcome of the fact that true Littersize, the number of kittens to be reared over the six-week focal period, was approximately the same for all females, ranging around 1 to 2 per female. Regardless of the choice of allomother, the Communal Littersize was raised by a regular increment of two for each additional female (the median value over all females, regardless of Side and Parity).

5.3.3. MATERNAL TIME BUDGET

As with the comparison between females on Sides A and B of the enclosure (see Section 5.2.3), only "viable" females were considered for these tests. In fact, Primiparas did not incur any non-viable litters; the main contributor was the Multiparous female, Jenny, who uniformly abandoned each of her 6 litters over the three breeding years. In fact, when each litter was considered separately, no differences were found between the experienced and inexperienced females (Figure 5.8; Week 1: $U= 30.5$, $Z= -1.704$, $p= .09$, $n= 7,16$; Week 2: $U= 38$, $Z= -1.023$, $p= .31$, $n= 7,15$; Week 3: $U= 38$, $Z= -1.022$, $p= .31$, $n= 7,15$; Week 4: $U= 36.5$, $Z= -.933$, $p= .35$, $n= 7,14$; Week 5: $U= 49$, $Z= -.247$, $p= .81$, $n= 7,15$; Week 6: $U= 45$, $Z= 0$, $p= 1$, $n= 6,15$; Weeks 1-3: $U= 32$, $Z= -1.445$, $p= .15$, $n= 7,15$; Weeks 1-6: $U= 32$, $Z= -1.07$, $p= .28$, $n= 7,13$).

When the tests were repeated using a mean score for each female, thus removing the two adult founding females who were Primiparas and who bred a second time, there was a small indication that Primiparous females tended to spend more time with their litters than did Multiparous females. This held true for Week 2 ($U= 10$, $Z= -2.222$, $p<0.05$, $n= 5,13$), Week 3 ($U= 8$, $Z= -2.420$, $p<0.05$, $n= 5,13$) and Week 6 ($U= 7$, $Z= -2.157$, $p<0.05$, $n= 4,13$), affecting the totals for Weeks 1-3 ($U= 11$, $Z= -2.124$, $p<0.05$, $n= 5,13$) and Weeks 1-6 ($U= 6$, $Z= -2.614$, $p<0.01$, $n= 5,13$). However, this

Figure 5.7.a

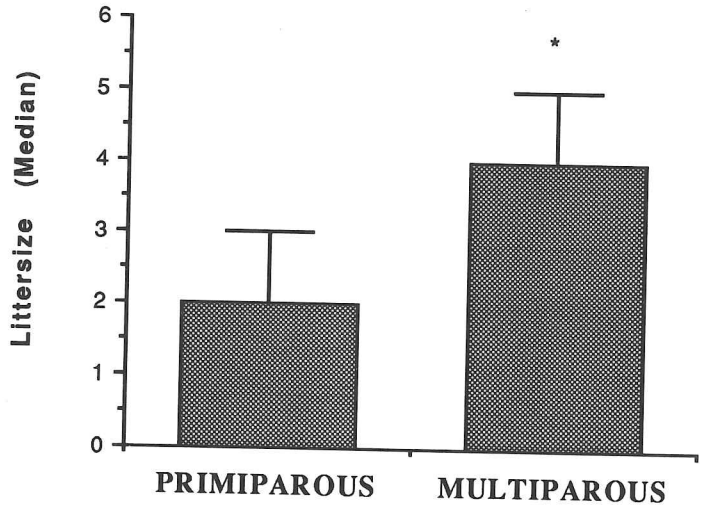

Figure 5.7.b

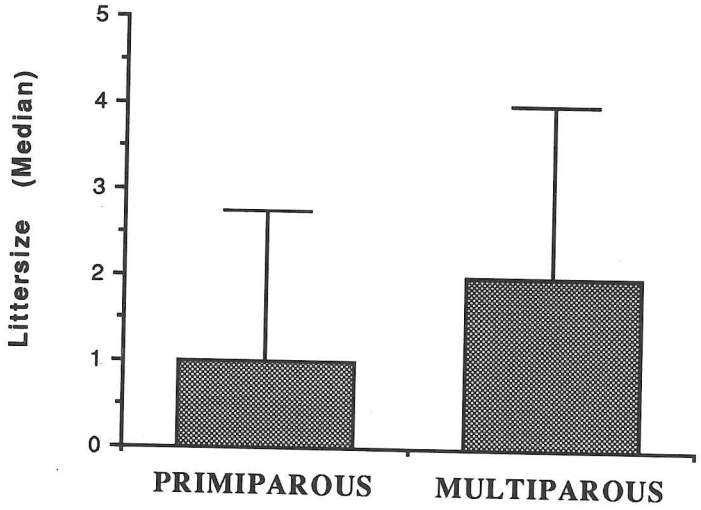

Figure 5.7: Differences between Primiparous and Multiparous mothers. Medians and interquartile ranges are given. (**a**) Littersize-at-Birth; (**b**) Littersize (equals Littersize-at-Birth minus any stillborns and kittens that died within two or three days of birth). *$p<0.05$, Mann-Whitney U-test.

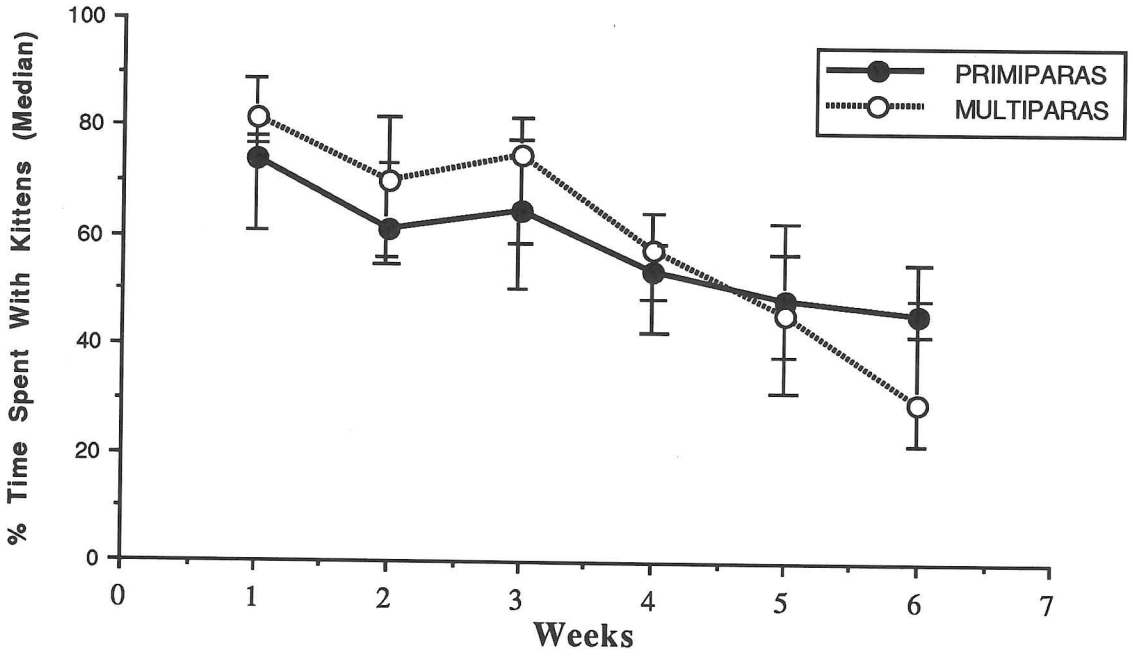

Figure 5.8: Maternal Time Budget comparisons between Primiparas and Multiparas. The weekly differences between the groups were non-significant with Mann-Whitney U-tests. Medians and interquartile ranges are shown.

analysis obscured the variation within Multiparous mothers and may distort the importance of Primiparas (as their scores are from single samples and not means).

5.3.4. KITTEN MORTALITY

When all litters were considered, including those that were non-viable due to early Mortality, a significantly higher incidence of Kitten Mortality was seen in Multiparas (Weeks 1-3: U= 42.5, Z= -2.557, $p<0.05$, n= 7,30, Weeks 1-6: U= 38, Z= -2.571, $p<0.01$, n= 7,30; To 4 Months: U= 6, Z= -1.992, $p<0.05$, n= 2,28; Figure 5.9). However, if only those litters that were viable and raised to six weeks were included, Kitten Mortality did not differ between Primiparous and Multiparous mothers (Weeks 1-3: U= 42.5, Z= -.976, p= .33, n= 7,16; Weeks 1-6: U= 38, Z= -1.278, p= .20, n= 7,16; To 4 Months: U= 6, Z= -1.295, p= .20, n= 2,14). This was not surprising, as there was effectively no difference in Littersize or Time Budgets between the females; it is interesting to note, however, that inexperienced mothers apparently incur no additional reproductive costs. In fact, Primiparas have smaller litters initially, unlike their Multiparous counterparts, so suffer even less from neonate mortality.

Again, it seems likely that Maternal Style, to be discussed in the next Section, may play an influential role; when all females were considered, Primiparas and Multiparas differed significantly in the Type of Care given to litters (U= 60.5, Z= -1.993, $p<0.05$, n= 7,30), in that most Primiparous females were Communal. This difference disappeared when only viable litters were included (U= 46.5, Z= -.834, p= .40, n= 7,16), perhaps because the majority of all litters that were shown care were Communal (76%).

5.3.5. NEST SITES

Primiparous and Multiparous mothers used similar numbers of Nest Sites over the first three weeks (U= 45.5, Z= -.718, p= .47, n= 7,16), over the last three weeks (U= 34.5, Z= -.893, p= .37, n= 7,13), and therefore, also over the whole six week period (U= 42.5, Z= -.24, p= .81, n= 7,13)(Figure 5.10). The explanation probably lies with the style of maternal care, to be discussed in Section 5.4.5, in that there is a significant effect of Type of Care on Nest Sites, and most viable litters (whether of a Primipara or a Multipara) were communally reared. When only Parity is considered, Nest Site use does not differ (Primiparas- Weeks 1-3: median=4; Weeks 4-6: median=3; Weeks 1-6: median=7; Multiparas- Weeks 1-3: median=3; Weeks 4-6: median=4; Weeks 1-6: median=8).

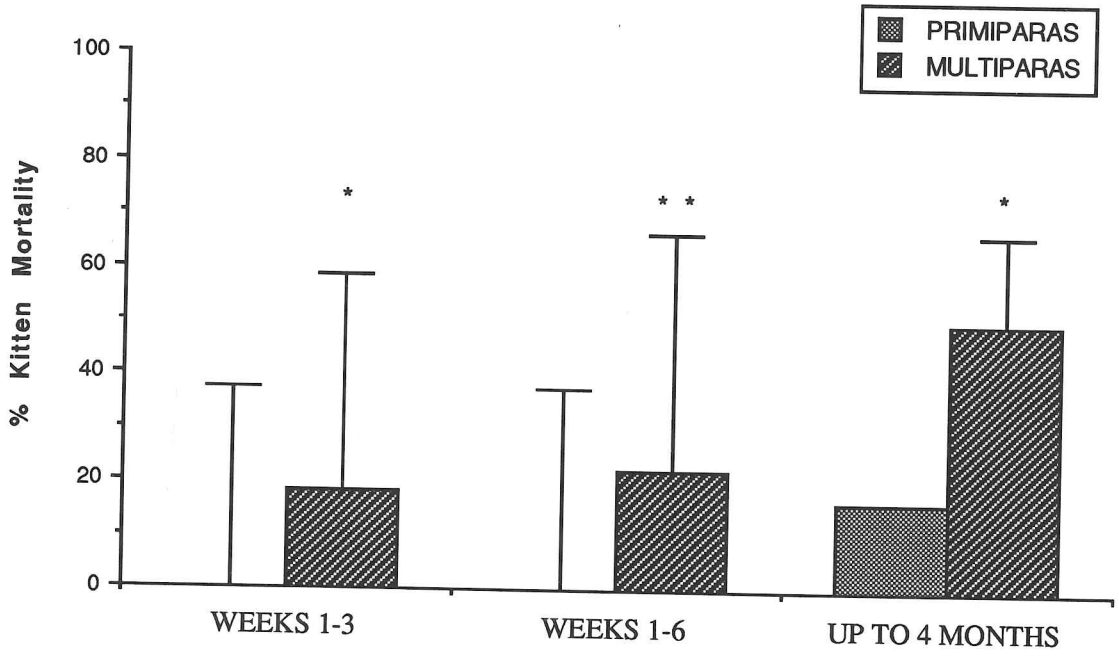

Figure 5.9: A comparison of the Kitten Mortality rates between the litters of Primiparous and Multiparous mothers. These were found for three different time periods, the first three weeks after birth (Weeks 1 to 3), the first six weeks after birth (Weeks 1 to 6), and the first four months after birth (Up to 4 Months). Values were calculated as the proportion of kittens per litter that died within each time period. Medians and interquartile ranges are shown. Where the median was zero, interquartile ranges stem from the x-axis. *$p<0.05$, **$p<0.01$, Mann-Whitney U-tests.

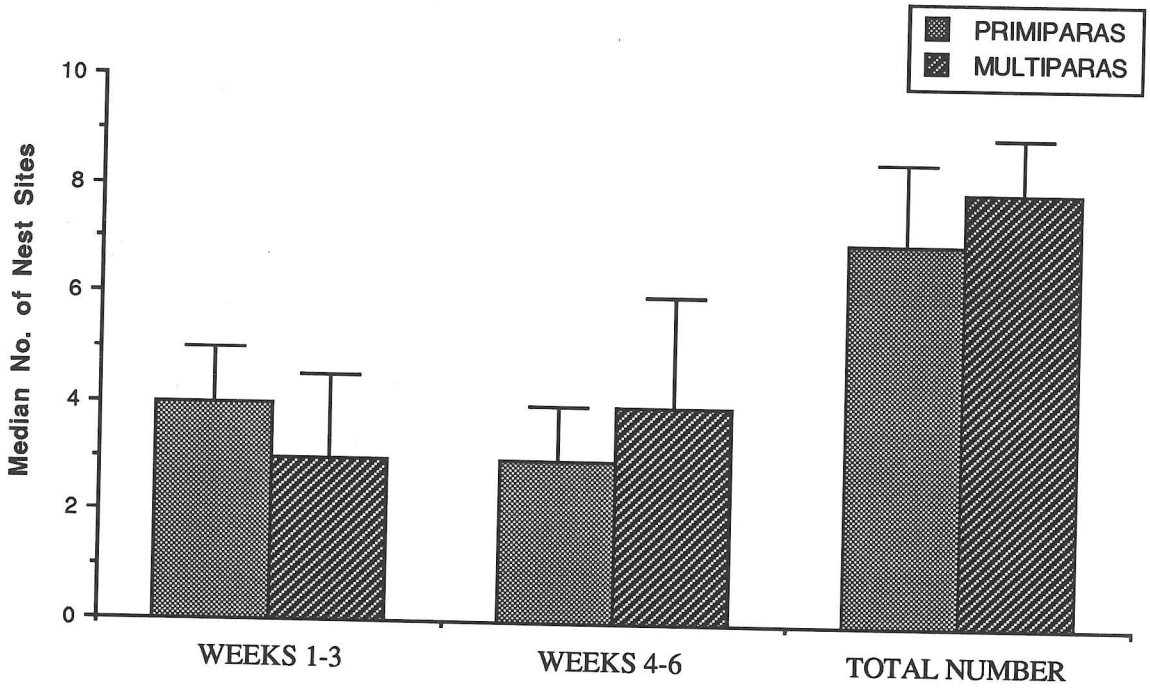

Figure 5.10: The number of Nest Sites used by Primiparous and Multiparous mothers. Medians and interquartile ranges are shown. The differences between the two groups were non-significant using Mann-Whitney U-tests.

5.3.6. OTHER PARITY CATEGORIES

When the litters are divided by the actual Parity of the mother, and not just lumped as Primiparous and Multiparous, many of the results are masked. Kruskal-Wallis tests were performed to differentiate between levels of maternal experience, ranging from first litters to ninth litters (median=4). Differences due to Parity were not found among the females, although analysis suggested that Time Budgets for viable litters (Week 3: H= 12.129, p= .059, df= 6; Weeks 1-3: H= 12.477, p= .052, df= 6) and Date of Birth (H= 14.317, p= .07, df= 8) might vary somewhat with Parity. As seen in the previous sections, Primiparas and Multiparas differed little in most reproductive variables; if so few things vary between inexperienced and experienced individuals, it seems unlikely that different notional levels of experience will differ to any substantial degree. Maternal experience appears to have little effect on the timing, substance or outcome of any individual reproductive effort. The data from this study show that a new mother seems to have the same chance of rearing a successful litter as an older mother; perhaps a small initial litter allows some variation in methods without being lethally costly, and later, larger litters are benefited by the experience. Type of Care also plays some role in the process, as will be discussed in the next section (Section 5.4).

5.4. MATERNAL STYLE: Solitary versus Communal

5.4.1. DATE OF BIRTH

When all litters were included, those born earlier in the season tended to be raised Communally (median=120 days), while later litters were Solitary (median=179.5 days). This difference was statistically significant (U= 104.5, Z= -2.022, $p<0.05$, n= 18,19; Figure 5.11.a). There appeared to be some influence on Care due to synchronous oestrus and birth dates, so the effect of clumping of birth dates was tested. The number of days separating pairs of birth dates was calculated (only those from the same group, as these females were able to choose Solitary versus Communal behaviour with regard to the other female), and the Type of Care noted for each pairing. Using a Mann-Whitney U-test to distinguish between Communal and Solitary litters, a significant difference was found (U= 54, Z= -3.386, $p<0.001$, n= 16,20); where Dates of Birth were separated by a few days (median=2), litters tended to be reared Communally, and where there was a larger gap between Dates of Birth (median=18.5) litters were Solitary. The difference between Solitary and Communal females may not be instigated by the individual mothers, but may be a circumstantial outcome of more or less synchronised reproductive

Figure 5.11.a

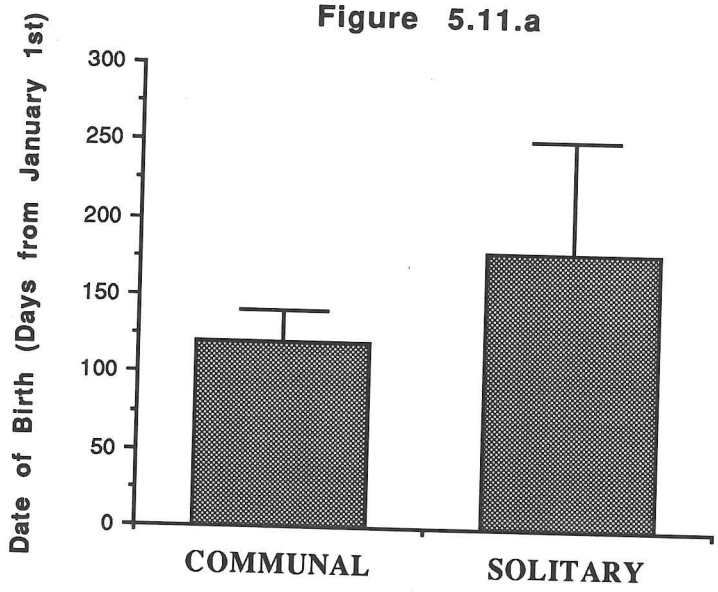

Figure 5.11.b

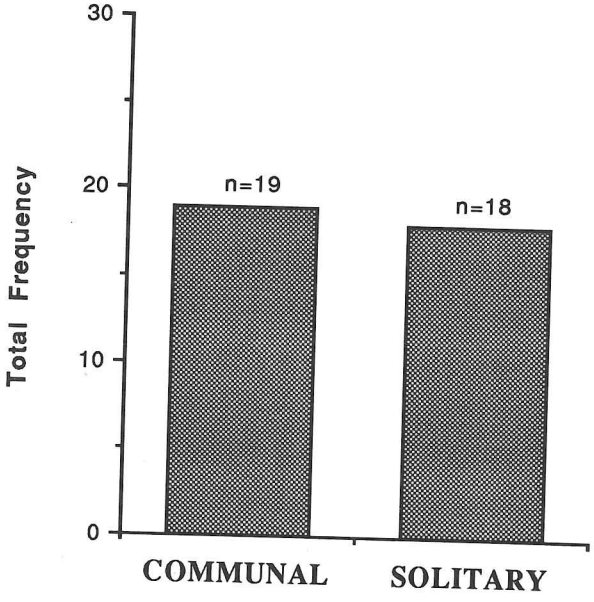

Figure 5.11.c

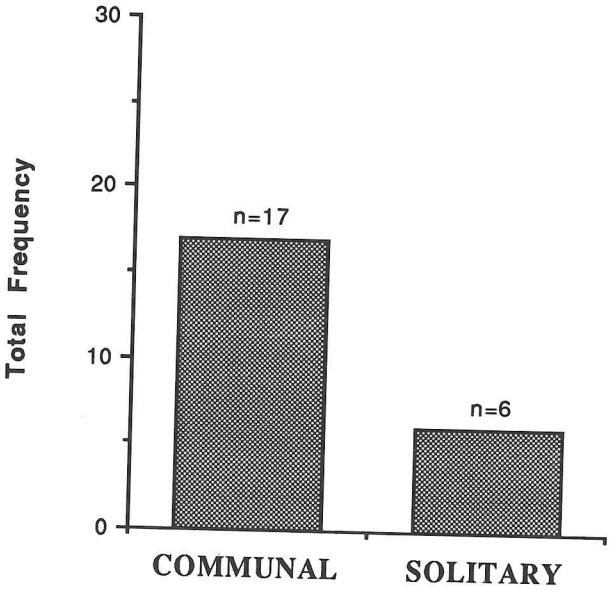

Figure 5.11: Differences between Communal and Solitary litters. (**a**) Date of Birth (showing the medians and interquartile ranges); (**b**) The distribution of Types of Care over all litters born; (**c**) The distribution of Types of Care over viable litters (those that survived the first two or three days after birth).

cycles. Overall, more litters were raised by Communal mothers than by Solitary ones (Figure 5.11.b), and the difference remains when only viable litters are compared (Figure 5.11.c).

The situation is complicated still further by the presence of two Communal tactics: litters which were Communal from birth (e.g. are born in the same nest, often on the same day) and those which became Communal later (e.g. were brought to a communal nest some days after birth, often weeks later). If the comparison is repeated between the Dates of Birth of Solitary and Communal litters, making the distinction between types of Communal care, using a Kruskal-Wallis test, the difference still holds true ($H= 12.792$, $p<0.01$, $df= 2$); in fact, litters which became Communal later were even more clumped in birth date than those born into a Communal nest. This was probably an effect of the 1987 birth season, in which three females had litters within 3 or 4 days, but only pooled them three weeks later.

5.4.2. LITTERSIZE

Solitary and Communal litters did not differ in terms of Littersize-at-Birth ($U= 113.5$, $Z= -.723$, $p= .47$, $n= 14,19$; Figure 5.12.a). However, when it came to the actual Littersize reared, Communal females had significantly larger litters (median=2, versus Solitary median=0.5; Mann-Whitney $U= 90.5$, $Z= -2.485$, $p<0.05$, $n= 18,19$; Figure 5.12.b). Solitary litters appeared to suffer higher mortality around parturition, whether in the form of stillbirth or neonatal death. This was undoubtedly biased by the presence of Jenny, who, as mentioned earlier, uniformly neglected 6 litters classed as Solitary. When she was removed from the analysis, the difference in Littersize disappeared ($U= 75$, $Z= -1.606$, $p= .11$, $n= 12,19$).

Communal Littersize, the total number of kittens actually raised by any one female when sharing care of kittens with another mother, can be predicted to increase with the number of females contributing litters; therefore, it is unsurprising that Communal litters were larger than Solitary litters ($U= 40$, $Z= -4.026$, $p<0.001$, $n= 18,19$). The initial analysis was performed using the Communal Littersize for each female and each litter; if the test is repeated using a single datum for each Communal litter (rather than approaching from the perspective of each contributing mother), the difference is still significant ($U= 23.5$, $Z= -3.254$, $p<0.01$, $n= 18,9$).

5.4.3. MATERNAL TIME BUDGET

One hypothesis was that the presence of multiple females caring for Communal litters would allow each individual female to reduce her time investment in the

Figure 5.12.a

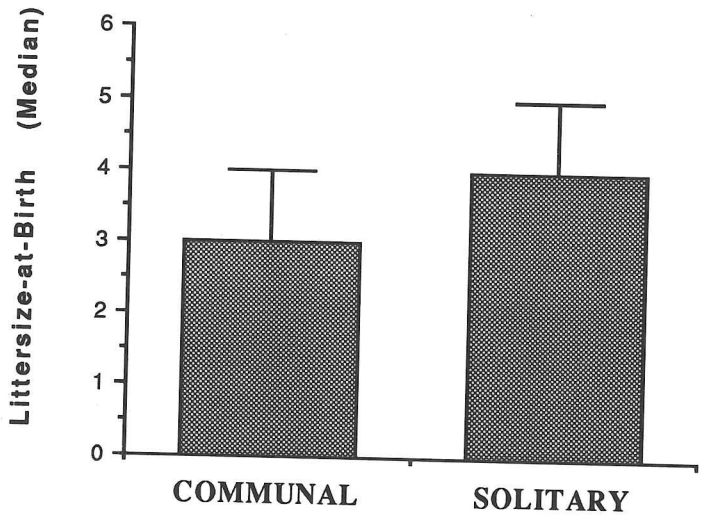

Figure 5.12.b

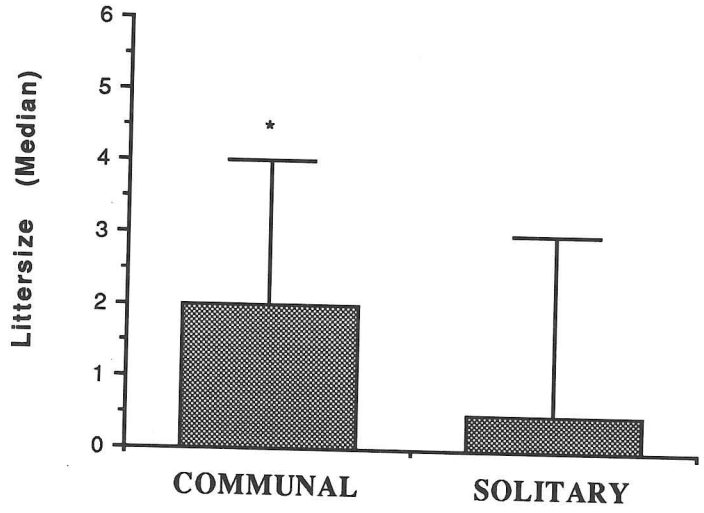

Figure 5.12: Differences between Communal and Solitary litters. Medians and interquartile ranges are given. (**a**) Littersize-at-Birth; (**b**) Littersize (equals Littersize-at-Birth minus any stillborns and kittens that died within two or three days of birth). *$p<0.05$, Mann-Whitney U-test.

kittens, thus predicting that Time Budget would be consistently greater in Solitary females. However, this was not the case for the cats in this study; there were no differences in Time Budget contingent on Type of Care, using two categories: Communal and Solitary (Week 1: U= 50.5, Z= -.035, p= .97, n= 6,17; Week 2: U= 35, Z= -.588, p= .56, n= 5,17; Week 3: U= 40, Z= -.196, p= .84, n= 5,17; Week 4: U= 39.5, Z= -.083, p= .93, n= 5,16; Week 5: U= 36, Z= -.885, p= .38, n= 6,16; Week 6: U= 27, Z= -1.402, p= .16, n= 6,15; Weeks 1-3: U= 42, Z= -.039, p= .97, n= 5,17; Weeks 1-6: U= 34, Z= -.66, p= .51, n= 6,14; Figure 5.13). When all three possible Care categories were used, Solitary, Communal from Birth and Communal Later, the groups still showed no significant differences in regard to Time Budgets.

If the difference in Communal Littersize is used instead of the Care categories, there is a slight indication that larger litters (Communal) received a little more attention as measured by the time each mother spends with the litter, only for Week 1 (Spearman r_s= .57, Z= 2.673, p<0.01, n= 23) and Weeks 1-3 (Spearman r_s= .416, Z= 1.905, p= .057, n= 22).

5.4.4. KITTEN MORTALITY

When all litters were considered, with abandoned litters classed as Solitary due to the attentions (or lack thereof) of a single mother, Solitary litters suffered a greater proportion of Mortality over all three time periods (Weeks 1-3: U= 83, Z= -2.821, p<0.01, n= 18,19; Weeks 1-6: U= 79, Z= -2.96, p<0.01, n= 18,19; To 4 Months: U= 59, Z= -2.259, p<0.05, n= 18,12). However, if only viable litters, those that received care, were included, Communal and Solitary litters showed no difference in Mortality (Weeks 1-3: U= 49, Z= -.152, p= .88, n= 6,17; Weeks 1-6: U= 50, Z= -.074, p= .94, n= 6,17; To 4 Months: U= 30, Z= 0, p= 1, n= 6,10; Figure 5.14). In fact, no "Solitary" litters were born into a Communal nest and then neglected, so it is not just the post-natal attention which can play a role, but also the circumstances into which a female presents kittens. Once care starts, there are no differential mortality costs for either reproductive style, probably due to the overall lack of difference in time spent with kittens. But it is still possible that a neglectful mother could enhance her reproductive success by giving birth in a previously occupied nest.

5.4.5. NEST SITES

Although Solitary and Communal females differed little in terms of most reproductive variables, the number of Nest Sites used by litters showed significant differences between the two groups. Over the six weeks, Communal litters occupied about

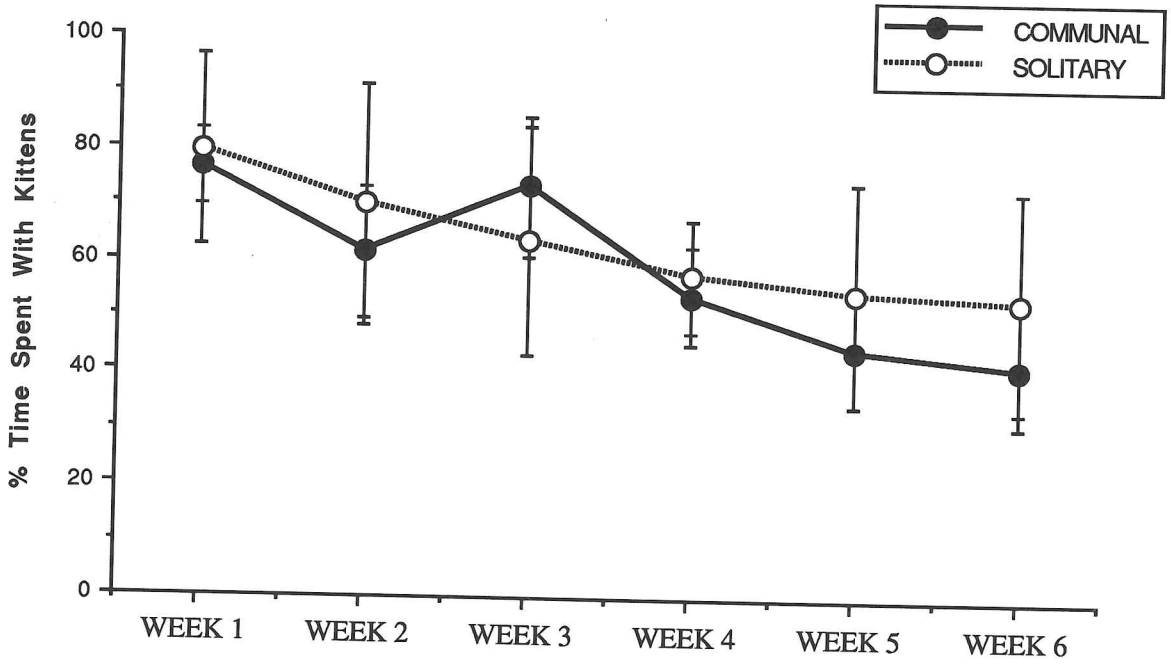

Figure 5.13: Maternal Time Budget comparisons between Solitary and Communal mothers. The weekly differences between the groups were non-significant with Mann-Whitney U-tests. Medians and interquartile ranges are shown.

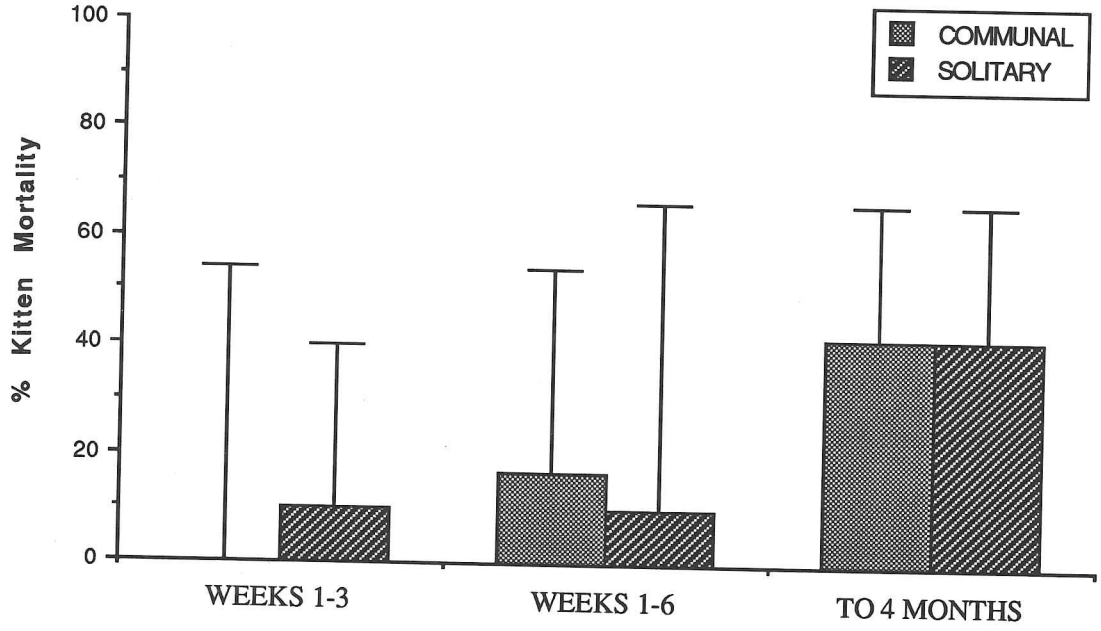

Figure 5.14: A comparison of the Kitten Mortality rates between the viable litters of Solitary and Communal mothers. These were found for three different time periods, the first three weeks after birth (Weeks 1 to 3), the first six weeks after birth (Weeks 1 to 6), and the first four months after birth (Up to 4 Months). Values were calculated as the proportion of kittens per litter that died within each time period. Medians and interquartile ranges are shown. Where the median was zero, interquartile ranges stem from the x-axis.

twice as many nests as did Solitary litters (Communal median=8, Solitary median=4; Mann-Whitney U= 9.5, Z= -2.703, p<0.01, n= 6,14; Figure 5.15). The main differences appeared over the first three weeks, when moving nest locations was completely dependent on the mother(s) (U= 11, Z= -2.866, p<0.01, n= 6,17); no significant difference was found over Weeks 4-6 (U= 19, Z= -1.944, p= .052, n= 6,14), although both the test statistic and the medians showed some disparity between Solitary (median=2.5) and Communal (median=4) litters.

Differences in Nest Site numbers may well reflect the constraints acting on a female when considering a change of nest location. A Solitary mother is solely responsible for her litter; if she decides to move nests, unless she has a single kitten, she must shuttle them one at a time, held in her jaws. This necessitates leaving both the original nest and the new one unguarded for some period of time. On the other hand, multiple females (whether mothers or not) can convey kittens more quickly and efficiently, rarely (if ever) leaving either nest unguarded with their alternating shuttling motion. This may be a coincidental result rather than an intentional tactic, but the effect is the same: kittens in Communal nests were rarely unguarded even when nest moves were taking place.

5.4.6. OTHER ASPECTS

The Date of Birth of litters was correlated with several other reproductive variables, such as Time Budget (when all litters are included): Week 3 (Spearman r_S= -.393, Z= -2.327, p<0.05, n= 36); Week 4 (Spearman r_S= -.419, Z= -2.443, p<0.05, n= 35); Week 5 (Spearman r_S= -.35, Z= -2.069, p<0.05, n= 36); Weeks 1-3 (Spearman r_S= -.372, Z= -2.198, p<0.05, n= 36); and Weeks 1-6 (Spearman r_S= -.401, Z= -2.303, p<0.05, n= 34). There was also, as noted earlier (Section 5.4.1), a relationship between Date of Birth and Type of Care (Spearman r_S= -.337, Z= -2.022, p<0.05, n= 37) over all litters born. When all litters were considered, Date of Birth was positively correlated with the various measures of Mortality; this effect remained significant when only viable litters were included in the analysis. Over Weeks 1-3, there was some indication that later litters had higher levels of Mortality (Spearman r_S= .388, Z= 1.822, p= .07, n= 23); the effect strengthened over Weeks 1-6 (Spearman r_S= .514, Z= 2.411, p<0.05, n= 23) and was still present when Mortality over the first 4 Months was considered (Spearman r_S= .563, Z= 2.181, p<0.05, n= 16).

Littersize also had an effect on a few variables. Littersize-at-Birth was positively correlated with Time Budget in Week 1 (viable litters only; Spearman r_S= .535, Z= 2.508, p<0.05, n= 23; Figure 5.16.a) in that mothers may respond to the birth of a larger litter by spending more time with them initially. However, the correlation disappeared for Littersize, and it is likely that females were quick to adjust their efforts as

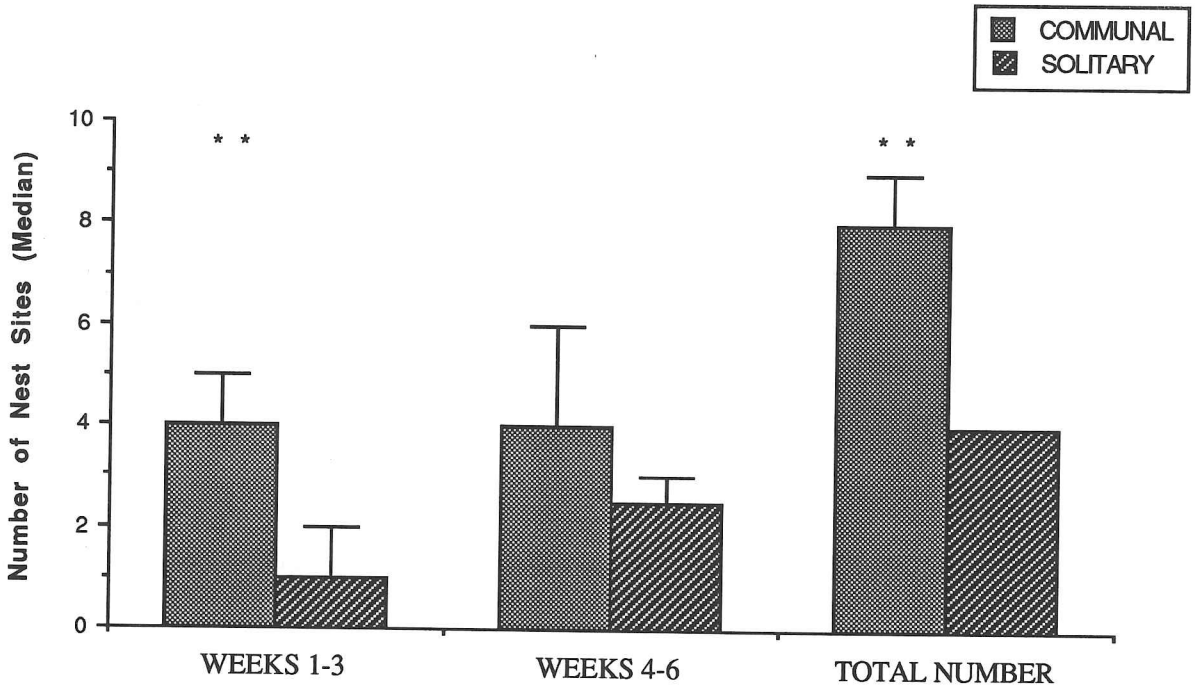

Figure 5.15: The number of Nest Sites used by the litters of Solitary and Communal mothers. Medians and interquartile ranges are shown. The third interquartile for Weeks 1 to 6 (Total Number) Solitary litters was the same as the median, hence the absence of a range indicator. **p<0.01, Mann-Whitney U-test.

Figure 5.16.a

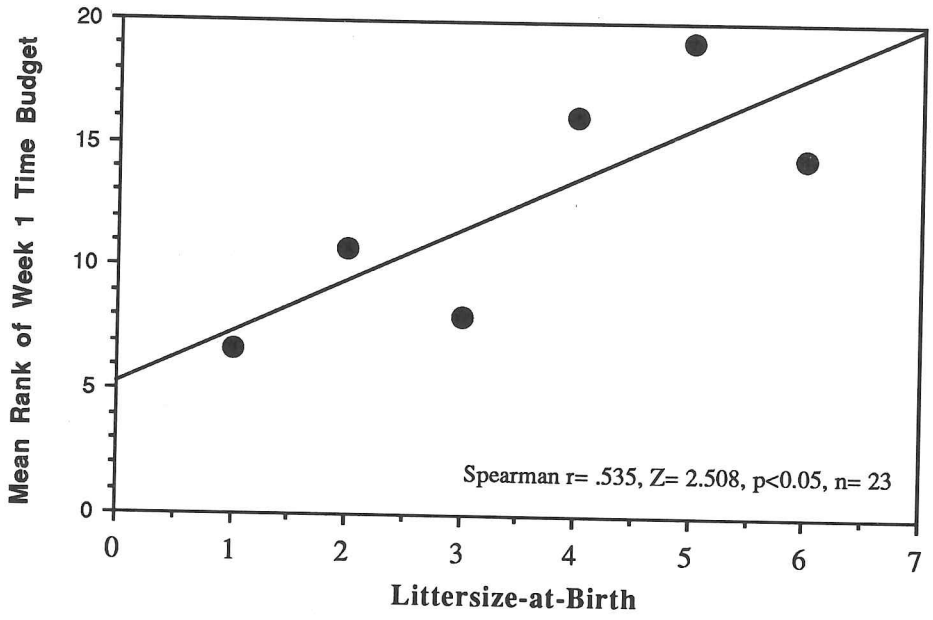

Figure 5.16.a: The correlation between Littersize-at-Birth and the Time Budget in Week 1. The test statistics are given in the lower right corner, from Spearman Rank Correlation.

Figure 5.16.b

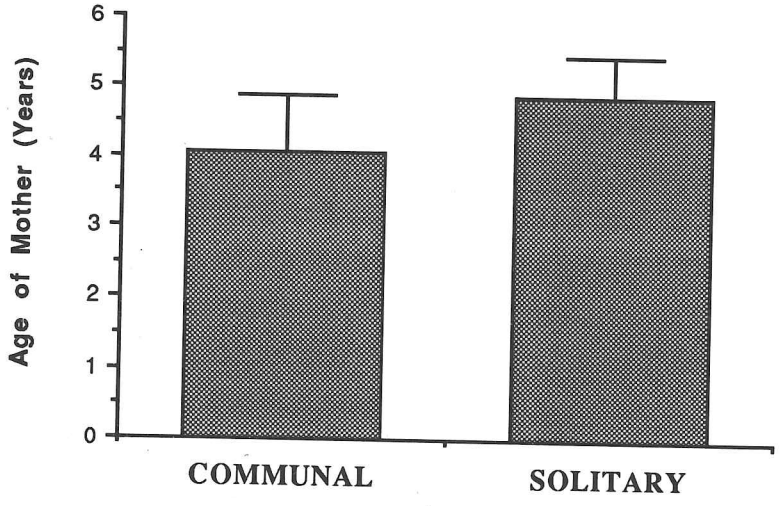

Figure 5.16.b: A comparison of Maternal Age between Communal and Solitary mothers. The difference was non-significant using a Mann-Whitney U-test (U= 39, Z= -.84, p= .40, n= 6 Solitary, 17 Communal).

the number of kittens in each litter stabilised over the first few days. Only long-term Mortality (to 4 Months) was correlated with Littersize (Spearman r_S= -.556, Z= -2.153, $p<0.05$, n= 16), such that larger litters corresponded to lower proportional mortality. Communal Littersize was similar to Littersize-at-Birth, in that it was positively correlated with Time Budget in Week 1 (Spearman r_S= .57, Z= 2.673, $p<0.01$, n= 23). One possibility was that the drop in littersize pursuant to birth and stillbirth acted as a stimulus for females to "seek out" additional kittens (in the form of Communal litters) to supplement the reduced number of kittens; thus Littersize-at-Birth and Communal Littersize might have been related to one another and to early Time Budget.

Maternal Parity and Type of Care appear to be having an interactive effect on the data in that Primiparas tended to be Communal. But overall, there was no age difference between Communal and Solitary mothers (Figure 5.16.b). It was not possible to test these two variables together, as non-parametrics have no equivalent of a two-factor Anova, but the interaction between the two variables is discussed in Section 5.10.

5.5. INDIVIDUAL VARIATION

5.5.1. TYPE OF CARE

Mothers showed an enormous degree of variation in the style of maternal Care, both within and between individuals. One female could show both Solitary and Communal care, for different litters. Some females raised only Solitary litters over the 3-year study (e.g. Daisy, n=2), while others were consistently Communal (e.g. Becky, n=3). The majority showed examples of each method, probably depending upon the circumstances around the birth, such as clumping of Dates of Birth. Because of the complicating factors within each female, inter-individual differences were analysed using means; for each female, separate means were calculated, for each variable, over her Solitary litters versus her Communal litters.

5.5.2. MATERNAL TIME BUDGETS

Using mean scores, Time Budgets showed no significant differences among females (Week 1: H= 14.144, p= .36, n= 13; Week 2: H= 16.254, p= .24, n= 13; Week 3: H= 16.679, p= .21, n= 13; Week 4: H= 17.185, p= .19, n= 13; Week 5: H= 17.246, p= .19, n= 13; Week 6: H= 14.123, p= .29, n= 12; Weeks 1-3: H= 15.872, p= .26, n= 13; Weeks 1-6: H= 16.941, p= .20, n= 13). Overall, there appeared to be no major differences among females, despite the large variation within individuals.

5.5.3. KITTEN MORTALITY

As with Time Budgets, no substantial differences were found among the females over any time period; Mortality over Weeks 1-3 (H= 13.36, p= .42, df= 13), Weeks 1-6 (H= 14.074, p= .37, df= 13) and the first 4 Months (H= 7.424, p= .49, df= 8) showed no inter-individual disparity. These means accounted for all litters, including those that showed complete mortality following birth, which affected Calico, Poppy, Tessa and Jenny.

5.5.4. NEST SITES

When the mean number of Nest Sites (over each time period) was used for each female, no significant differences were found among the various mothers (Weeks 1-3: H= 14.265, p= .28, df= 12; Weeks 4-6: H= 14.609, p= .26, df= 12; Weeks 1-6: H= 15.239, p= .23, df= 12). Other factors were subsequently examined to see if they could explain any of the observed variation seen in the number of Nest Sites; the following analyses returned to the use of separate litters as independent datum points to remove the averaging effect. Communal Littersize did not affect Nest Sites (Weeks 1-3: H= 8.857, p= .18, df= 6; Weeks 4-6: H= 5.034, p= .41, df= 5; Weeks 1-6: H= 6.468, p= .26, df= 5). Time Budgets, the proportion of time mothers spent with kittens, appeared to have no effect on number of Nests (or vice versa), using Spearman Rank Correlation Coefficients. By the same token, numbers of Nest Sites had no significant influence on Kitten Mortality (using a Kruskal-Wallis analysis), although there was a slight indication that the number of Nests over Weeks 1-3 affected Mortality over Weeks 1-3 (H= 10.106, p= .07, df= 5); it is unlikely that this was anything more than a weak association.

5.5.5. ALLOMOTHERING

Allomothering, or the provision of care by non-mothers, was a strong feature in the two cat groups studied here. The majority of litters born received some level of cooperative help, which varied hugely in its form. The most common occurrence was the pooling of two or more litters from birth; once, this involved a mother and daughter, but more commonly pooling was found in unrelated females (although they might have been so familiar as to be assumed to be kin), including two Primiparous females who were Communal littermates (they may have been sisters or half-sisters, due to the presence of only one breeding male). Sometimes litters were pooled several weeks after birth.

Another form that care took was helping; the identity of helpers was curious and raised many questions. An old female, well past her own reproductive prime, who was mated but never became pregnant, was one of the most dedicated helpers, involved in the rearing of more than half the litters born to her group. In 1987, this old "nurse", Laura, was aided by a young nulliparous female, Wanda, who bred successfully herself in following years. Other helpers included young males (also seen by Macdonald 1983); in 1989, Calico was aided by Catkin, her son born 2 years previously, and by Duffy, the year-old male offspring of Daisy (a Solitary mother). Other young cats, females, also helped briefly, but not to the same extent as the males for this particular litter. Where juvenile females or males were the helpers, the litter was not classified as Communal, as the degree and amount of help seemed unequal to that provided by other females, in that males appeared somewhat less attentive to kittens, as did young (e.g. juvenile) females.

Within some pairs of Communal mothers, a striking disparity was seen in the time spent with kittens; this was especially prominent in 1988, between Poppy and Katrina (Figure 5.17.a). Katrina gave birth in the nest occupied by Poppy and her 4-day-old kittens; after a short period of joint care, Katrina left the nest and showed exclusive interest in an older Communal litter elsewhere. Poppy was left to raise all the kittens alone and, despite the lack of reciprocal help from Katrina, reared and responded to all the kittens as her own.

Sometimes, the pooling of litters had a purely detrimental effect on the mothers and kittens involved. Such a case was the Communal litter of Poppy and Tessa in 1989; Tessa entered Poppy's established nest and gave birth within a day of Poppy's litter. Together, they had 11 kittens, which received care for a day or two; the litter was moved to a new nest, but both females continued to lie in the original nest with a new litter belonging to Becky. The kittens died within two days, with no observed attendance by the mothers despite prolonged periods of plaintive mewing. The only logical explanation, based partly on behavioural observation, was that one mother, probably Tessa, moved the litter; the other mother, Poppy, was unable to find them or was driven away by the mutual aggression between the two adults. This example is further discussed in Chapter 6.

Although females were tested for intra-individual differences with Communal and Solitary litters, the results showed little effect; only a couple of females actually raised litters under both conditions, and these were often reared with the aid of non-breeding helpers (e.g. Calico,1989), or were born at one extreme of the breeding season (e.g. Calico,1988,1989, Poppy,1987). Most females were either consistently Solitary (e.g. Daisy) or consistently Communal (e.g. Becky). As a result, it was very difficult to test the theory that an individual mother could reduce her reproductive effort by pooling litters with another female. Based on anecdotal evidence, several notable examples stand out. Calico did spend less time with her Communal litter (Figure 5.17.b); however,

Figure 5.17.a

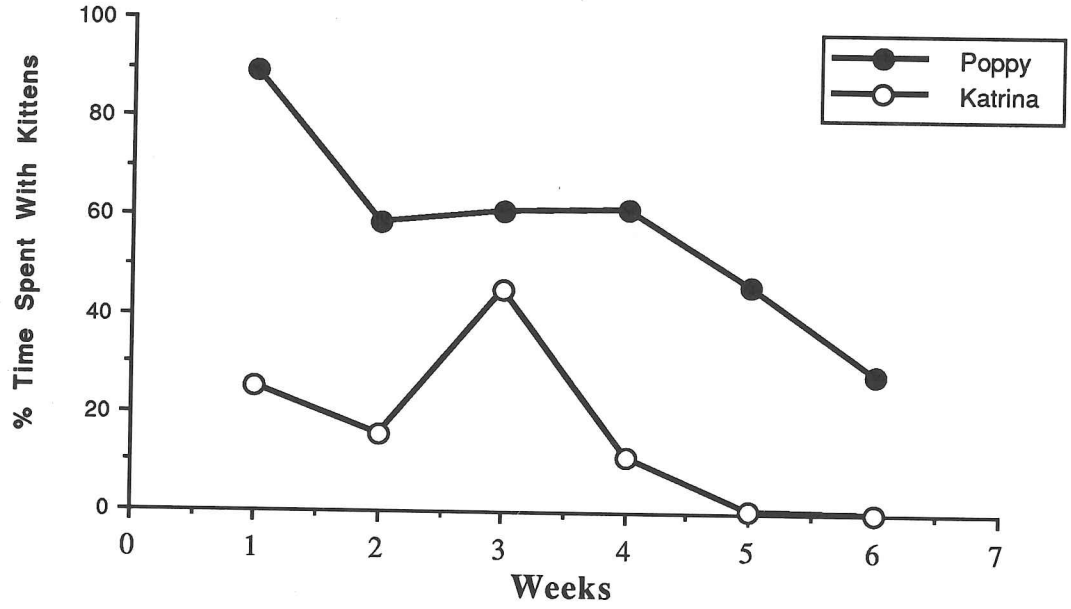

Figure 5.17.b

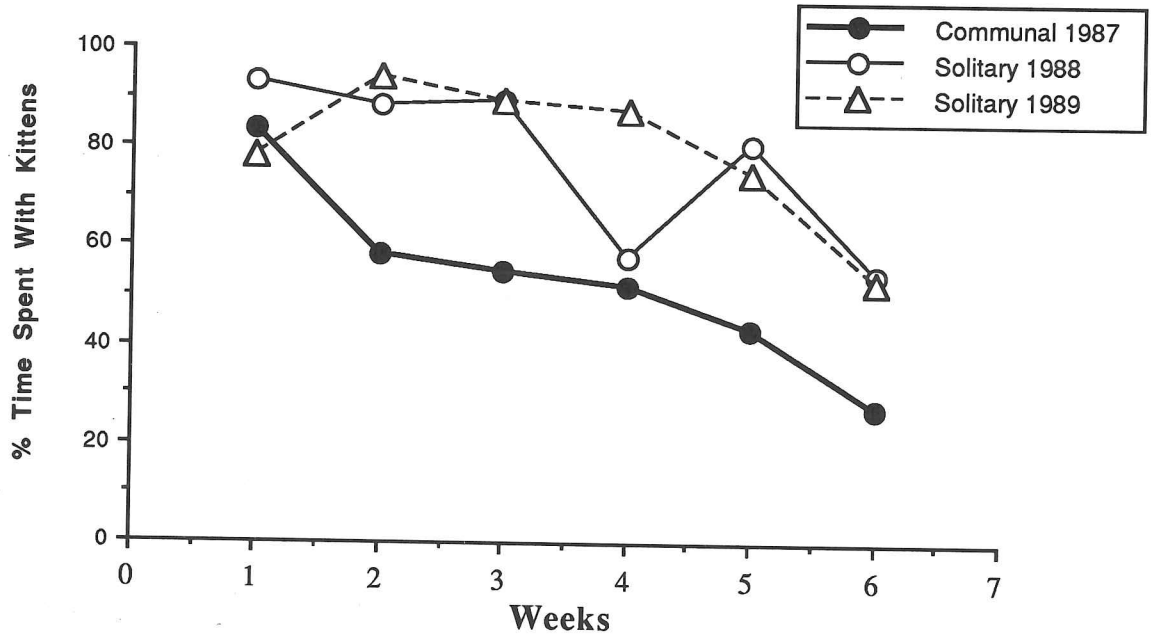

Figure 5.17: Individual differences in Maternal Time Budget. Values are expressed as the proportion of observation time that females were with their kittens over the first six weeks after the birth of the litter. (**a**) Two Communal mothers, Poppy and Katrina, in 1988; (**b**) Calico and her Time Budget for three litters over 1987 to 1989, with varying Types of Care.

Figure 5.17.c

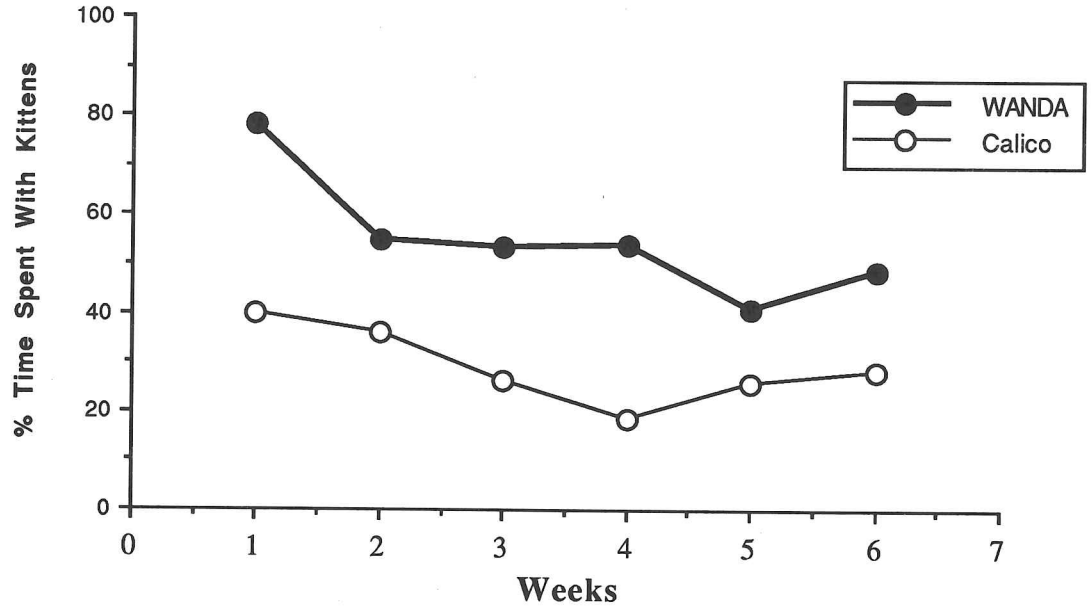

Figure 5.17.d

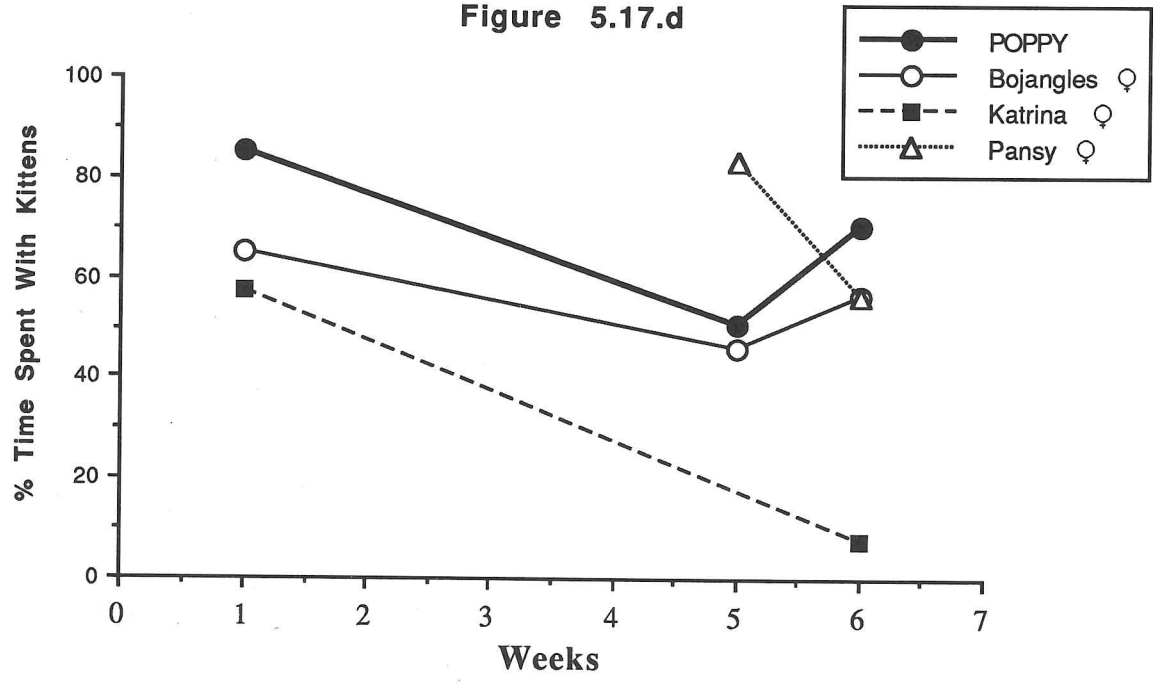

Figure 5.17: Individual differences in Maternal Time Budget. Values are expressed as the proportion of observation time that females were with their kittens over the first six weeks after the birth of the litter. (**c**) Two Communal mothers, Wanda and Calico, in 1988 with Wanda's litter; (**d**) Poppy and her helpers for a second litter in December 1987.

Figure 5.17.e

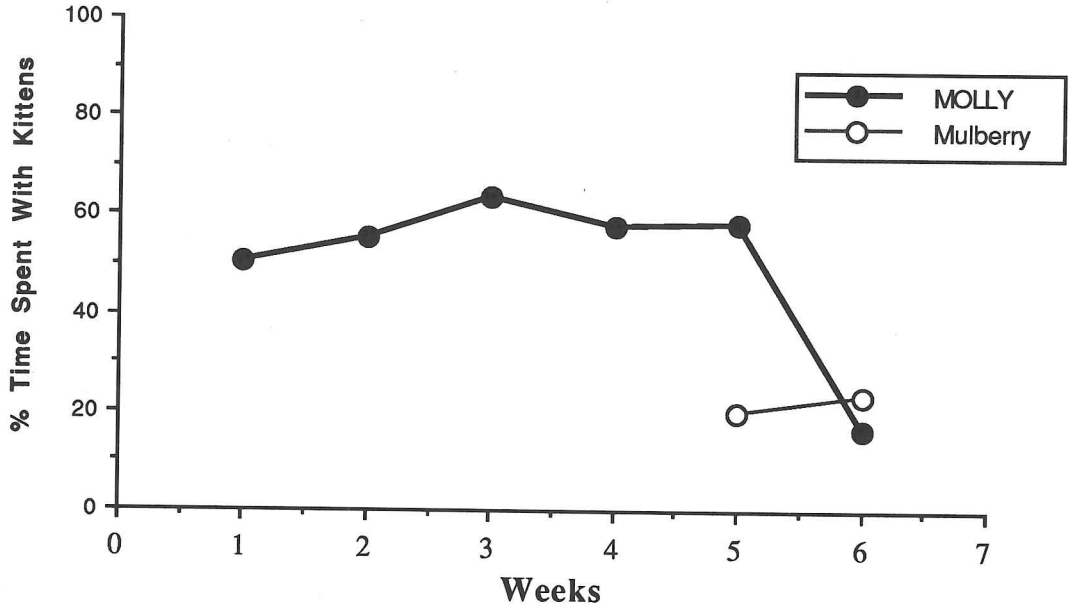

Figure 5.17.f

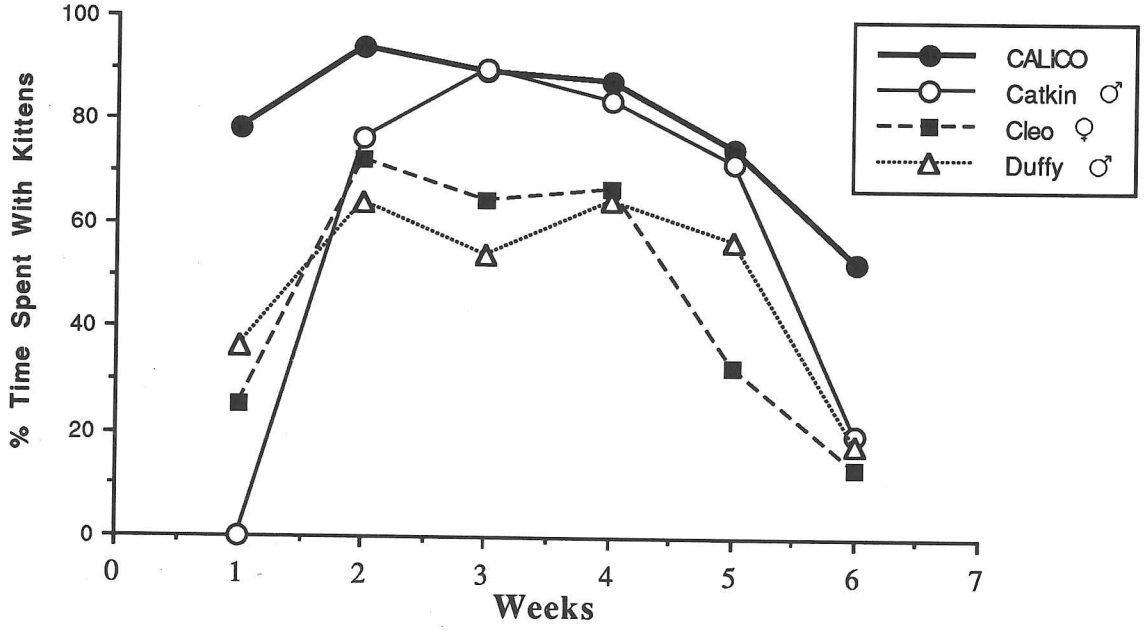

Figure 5.17: Individual differences in Maternal Time Budget. Values are expressed as the proportion of observation time that females were with their kittens over the first six weeks after the birth of the litter. (e) A Solitary mother, Molly, and her helper (and daughter), Mulberry in 1988; (f) A Solitary mother, Calico, and her helpers (and offspring) in 1989.

it only became Communal after a few weeks, yet her time with the litter dropped from Week 2 (perhaps preparatory to the move, or unrelated). Also, for her two "Solitary" litters (in 1988 and 1989), Calico was joined by non-breeding helpers, including Wanda before she had her own litters (Wanda raised both her own litters as Communal with Calico's much older offspring). No other females showed a clear difference between Time Budgets, and that seen in Calico's may be simply due to inter-litter variation.

A second hypothesis was that individual females could substantially reduce their own efforts in a single litter by pooling with a second mother and leaving before the end of the kittens' dependent period. This relies on the goodwill and loyalty of the major care-giver, and requires either a lack of individual kitten recognition, close kinship or reciprocal altruism; otherwise, there is no guarantee that the burdened female will include the abandoned kittens in her maternal efforts. Despite a few graphic discrepancies (e.g. Poppy and Katrina,1988, Figure 5.17.a), there appears to be little support for this notion; it was, however, obvious that helpers spent less time with kittens than did the mothers (Figures 5.17.c-f), confirming the valid differences in the classification of "communal" (multiple mothers) versus "cooperative" (mother plus helpers) litters.

5.5.6. EFFECTS ON OTHER REPRODUCTIVE VARIABLES

When all litters were included as separate datum points as opposed to female means, the females showed a substantial difference in Parity (Kruskal-Wallis: $H= 25.363$, $p<0.05$, $df= 13$) and the attendant variable Mother Age ($H= 24.347$, $p<0.05$, $df= 13$). It was necessary to use each litter as a separate datum to avoid averaging out the females who bred several times over 3 years, and thereby reducing the actual contrast. The significant differences were obviously due to the females born into the colony who bred in 1989; these included females born in 1987 (Bojangles, Pippin and Mulberry) as well as two born in 1988 (Tycho and Bailey).

Returning to the analysis based on means (only for those females who bred more than once with each style of care, otherwise the score is actually a single datum), no individual difference in Date of Birth was found ($H= 12.803$, $p= .46$, $df= 13$), due to the birth synchrony noted earlier. Littersize-at-Birth ($H= 12.859$, $p= .46$, $df= 13$) and Littersize ($H= 10.141$, $p= .68$, $df= 13$) also failed to display significant differences based on mother's identity.

5.6. KITTEN DEVELOPMENT

Due to the secluded nature of nests, it was particularly difficult to systematically identify most features of development, e.g. growth (weight gain). However, in a number of more accessible litters, it was possible to note aspects such as when eyes opened, when kittens were first observed to be highly mobile and playing, when kittens first left the nest, and the first observation of ingestion of solid food (Table 2.4). These features are considered well-defined stages in development for cats (Hemmer 1979), and allow a modicum of comparison with other studies. Unfortunately, sample sizes are too small to allow firm testing, and the following results are used primarily as indicators.

5.6.1. MATERNAL INFLUENCES

Maternal identity did not have an effect on any of the four characters used to estimate kitten development (Figure 5.18): the day upon which Eyes Opened (Kruskal-Wallis H= 4.545, p= .21, df= 3); the day upon which kittens were first observed to be highly Mobile and playing (H= 6.578, p= .16, df= 4); the day upon which kittens first Leave Nest (H= 4.151, p= .25, df= 3); and the day upon which kittens were seen to first Eat Solids (H= 2, p= .37, df= 2). Therefore, individual mothers did not appear to vary broadly in aspects which might affect kitten development, such as milk quality and quantity.

5.6.2. DATE OF BIRTH

Date of Birth did not influence any of the four developmental estimators: Eyes Open (Spearman r_s= -.409, Z= -.915, p= .36, n= 6); Mobile/Play (r_s= -.012, Z= -.033, p= .97, n= 8); Leave Nest (r_s= -.112, Z= -.275, p= .78, n= 7); or Eat Solids (r_s= -1, Z= -1.413, p= .16, n= 3). Early births neither accelerated nor slowed kitten development in this study.

5.6.3. PARITY

Parity of mother did not influence the following measures used to estimate kitten development: Eyes Open (Kruskal-Wallis H= 3.636, p= .46, df= 4); Mobile/Play (H= 3.584, p= .47, df= 4); and Leave Nest (H= 5.745, p= .33, df= 5). Eat Solids was not testable as all samples (n=3) came from the litters of Multiparous mothers. Similarly,

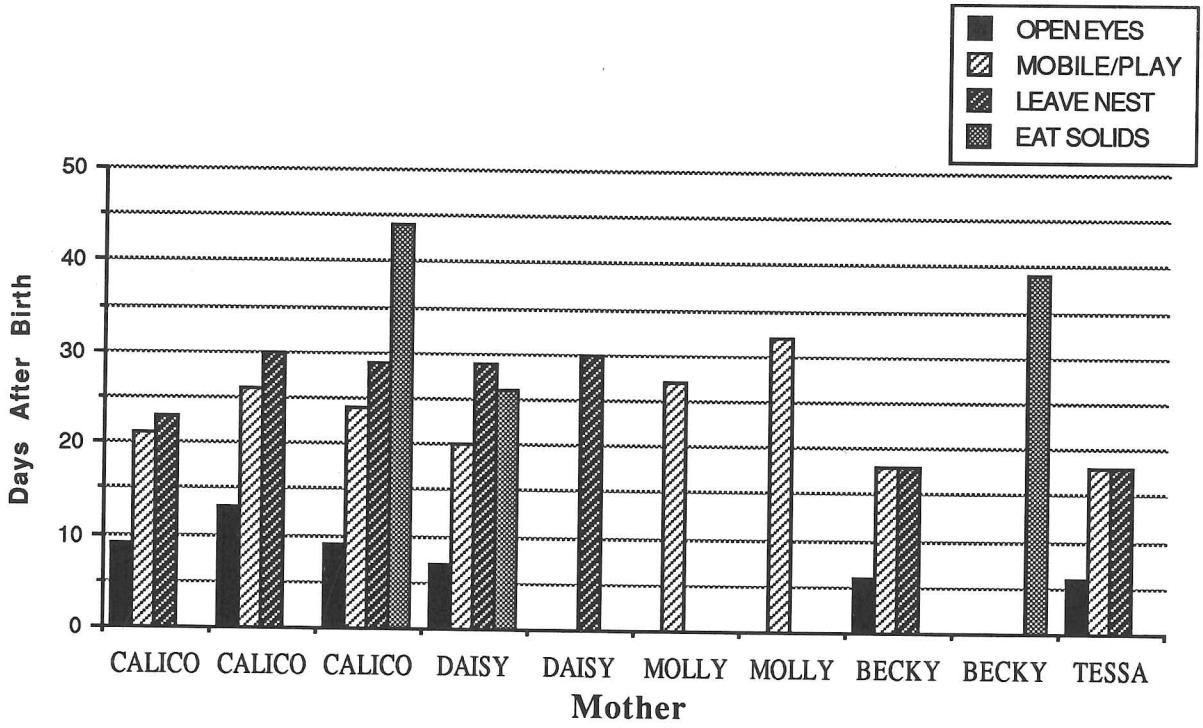

Figure 5.18: A summary of the recorded variables regarding kitten development. Each listing above is for a separate litter, although the same mother might be noted more than once. As a result of the difficulty in observing kittens, most litters were not seen for all four variables. The number of samples for each variable is given: Eyes Open - n=6; Mobile/Play - n=8; Leave Nest - n=7; Eat Solids - n=3. The differences between mothers were non-significant using Kruskal-Wallis tests.

Maternal Age was not related to the developmental variables: Eyes Open (Spearman r_S= .088, Z= .197, p= .84, n= 6); Mobile/Play (r_S= .229, Z= .606, p= .54, n= 8); Leave Nest (r_S= -.239, Z= -.585, p= .56, n= 7); or Eat Solids (r_S= .5, Z= .707, p= .48, n= 3). Therefore, maternal age and experience did not seem to affect the measures used as rough gauges of kitten development in this study.

5.6.4. LITTERSIZE

Littersize made no difference to the rate at which kittens developed (Eyes Open: Kruskal-Wallis H= 1.932, p= .75, df= 4; Mobile/Play: H= 5.208, p= .39, df= 5; Leave Nest: H= 2.226, p= .69, df= 4). Communal Littersize also failed to explain the variation in developmental features (Eyes Open: H= 4.659, p= .20, df= 3; Mobile/Play: H= 5.454, p= .14, df= 3; Leave Nest: H= 4.151, p= .25, df= 3). Eat Solids could not be tested as the only data coincidentally came from litters of the same size; small sample sizes prevented testing of Communal Littersize. Thus, sibling numbers had no apparent effect on these developmental measures in cats, despite indications (in rats) that more siblings might accelerate locomotion and certain adult-like behaviour (Moretto et al. 1986).

5.6.5. MATERNAL TIME BUDGETS

Spearman Rank Correlation Coefficient tests were used to examine the data for associations between Maternal Time Budget and kitten development. No significant relationships were found between any two combinations of Time Budget and development, indicating that maternal effort (as reflected by proportions of total time spent with litter) did not influence the aspects of kitten development in this study (Table 5.2). It would appear that, for these measures, there was no disparity among mothers in regard to overall effort (i.e. lactation). In other words, in as much as Maternal Time Budget was able to accurately estimate some level of input or "investment", it did not have any linear association with the four measures of kitten development.

5.6.6. TYPE OF CARE

Communal and Solitary litters differed little in regard to the days for Eyes Open (Mann-Whitney U= 1.5, Z= -1.348, p= .18, n= 3,3), Mobile/Play (U= 7, Z= -.15, p= .88, n= 5,3) and Eat Solids (U= 1, Z= 0, p= 1, n= 1,2). However, the Type of Care had a significant effect on the day upon which kittens first Leave (the) Nest (U= 0, Z= -2.181, $p<0.05$, n= 3,4), such that Communal kittens left the nest more than a week earlier than Solitary litters (Figure 5.19). It is doubtful that the effect was circumstantially

Table 5.2: Spearman Correlation Statistics for a Comparison of Maternal Time Budget and Kitten Development. A significant result would mean that the (ranked) Time Budget was linearly related with the (ranked) Kitten variable, e.g. that there was a linear association between the time mothers spent with kittens and the kittens' development.

Time Budget	Kitten Variable	n	r_s	Z	p
Week 1	Open Eyes	6	-.177	- .395	.69
Week 1	Mobile	8	-.407	-1.077	.28
Week 1	Leave Nest	7	-.367	- .899	.37
Week 1	Eat Solids	3	1	1.414	.16
Week 2	Open Eyes	6	.530	1.184	.24
Week 2	Mobile	8	.467	1.236	.22
Week 2	Leave Nest	7	.312	.764	.44
Week 2	Eat Solids	3	1	1.414	.16
Week 3	Open Eyes	6	.353	.790	.43
Week 3	Mobile	8	-.012	- .032	.97
Week 3	Leave Nest	7	.073	.180	.86
Week 3	Eat Solids	3	1	1.414	.16
Weeks 1-3	Open Eyes	6	.441	.987	.32
Weeks 1-3	Mobile	8	.144	.380	.70
Weeks 1-3	Leave Nest	7	.147	.360	.72
Weeks 1-3	Eat Solids	3	1	1.414	.16
Week 4	Open Eyes	6	-.177	- .395	.69
Week 4	Mobile	8	-.156	- .412	.68
Week 4	Leave Nest	7	-.422	-1.034	.30
Week 4	Eat Solids	3	1	1.414	.16
Week 5	Open Eyes	6	.441	.987	.32
Week 5	Mobile	8	.347	.919	.36
Week 5	Leave Nest	7	.018	.045	.96
Week 5	Eat Solids	3	.500	.707	.48
Week 6	Open Eyes	6	.618	1.382	.17
Week 6	Mobile	8	.539	1.426	.15
Week 6	Leave Nest	7	.642	1.574	.12
Week 6	Eat Solids	3	.500	.707	.48
Weeks 1-6	Open Eyes	6	.353	.790	.43
Weeks 1-6	Mobile	8	.275	.729	.47
Weeks 1-6	Leave Nest	7	.073	.180	.86
Weeks 1-6	Eat Solids	3	1	1.414	.16

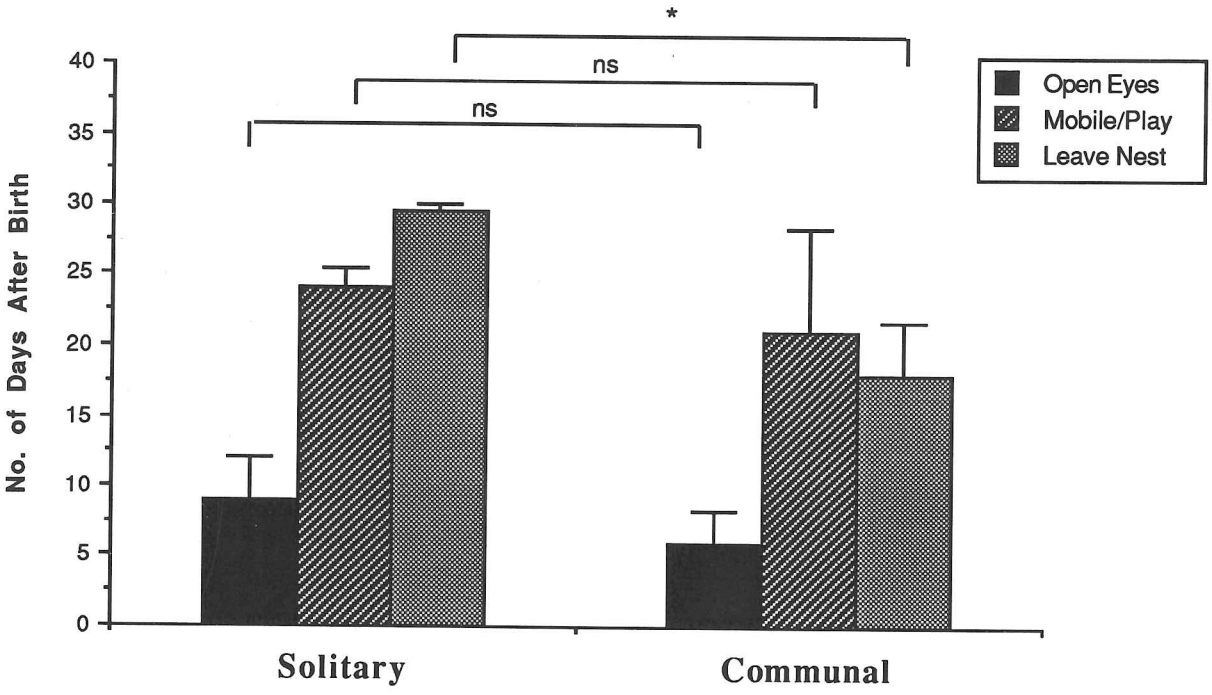

Figure 5.19: Differences between Solitary and Communal litters in terms of kitten development. Medians and interquartile ranges are shown. Eat Solids is not included, as small sample sizes prevented this particular analysis. ns = $p>0.05$, *$p<0.05$, Mann-Whitney U-test.

due to increased activity in the nest, or even to reduced space, as various measures of littersize appeared to have no effect on the timing of Leave Nest (Section 5.6.4).

5.6.7. NEST SITES

Spearman Rank Correlations were used to examine the relationship between numbers of Nest Sites and kitten development (Table 5.3). Nests over Weeks 4-6 and Nests over Weeks 1-6 were both found to influence the day kittens Leave (the) Nest; this was probably a result of the significant relationship between the Type of Care and the number of Nest Sites over these two intervals (see Section 5.6.6). It is not clear whether it was the Type of Care itself, manifested in some unmeasured form, or the number of Nest Sites, which influenced nest departures; frequent changes of nest over Weeks 4-6, when kittens are increasingly mobile, may involve kitten locomotion rather than maternal handling. In turn, this may increase either kitten locomotor strength or adventurousness; Communal kittens may be less intimidated by the environment outside the currently occupied nest and may therefore leave the nest earlier.

5.6.8. KITTEN MORTALITY

No relationship was found between the four measures of development and Mortality measured over the first 6 weeks (Open Eyes: Spearman r_S= .679, Z= 1.518, p= .13, n= 6; Mobile/Play: r_S= .412, Z= 1.089, p= .28, n= 8; Leave Nest: r_S= .16, Z= .393, p= .69, n= 7; Eat Solids: r_S= .5, Z= .707, p= .48, n= 3). It is possible that developmental retardation has few measurable effects until later in life.

5.7. REPRODUCTIVE SUCCESS

Another consideration which has not yet been discussed is the survival of individual kittens past the age of weaning. The aspects of Kitten Mortality discussed in the previous sections were centred around the relative survival of whole litters rather than the survival of individual kittens. Weaning in cats is generally thought to be complete by approximately 8 weeks (Ewer 1973; Dards 1979; Deag et al. 1988; Martin & Bateson 1988); in this study, reaching the age of 4 months or more was considered to be the criterion for post-weaning survival (as few cats were seen to die after this age). Not surprisingly given the diversity discussed earlier (Section 5.5), a huge amount of individual variation was seen in the mothers, both in respect to the total number of kittens born over

Table 5.3: Spearman Correlation Statistics for Number of Nest Sites and Kitten Development. A significant probability level indicates that the (ranked) Number of Nest Sites (over any period) was linearly related with the (ranked) Development Variable. For example, the relative date of Leaving the Nest decreases as the (relative) Number of Nest Sites in Weeks 4-6 increases.

Nest Sites	Development Variable	n	r_s	Z	p	
Weeks 1-3	Open Eyes	6	-.572	-1.279	.20	
Weeks 1-3	Mobile/Play	8	-.315	- .833	.40	
Weeks 1-3	Leave Nest	7	-.563	-1.379	.17	
Weeks 1-3	Eat Solids	3	0	0	1	
Weeks 4-6	Open Eyes	6	-.715	-1.599	.11	
Weeks 4-6	Mobile/Play	8	.259	.686	.49	
Weeks 4-6	Leave Nest	7	-.912	-2.234	<0.05	*
Weeks 4-6	Eat Solids	3	-.500	- .707	.48	
Total	Open Eyes	6	-.727	-1.626	.10	
Total	Mobile/Play	8	-.073	- .192	.84	
Total	Leave Nest	7	-.849	-2.080	<0.05	*
Total	Eat Solids	3	-.500	- .707	.48	

the three year study period (Figure 5.20.a), ranging from 1 to 24, and in the survival of these kittens (Figure 5.20.b), ranging from 0 to 12. The data can be viewed in several ways: Bojangles, Tycho, Daisy, Becky and Wanda had the highest overall percentage survival; Becky, Calico and Daisy contributed the greatest number of kittens to the population (Table 5.4).

When the total number of surviving kittens was divided by the number of breeding years for each female, a rough measure of "reproductive success" was derived (Kerby 1987). This was constrained by the fact that a single fragment of reproductive time was available, but it gave some means by which to compare females. A second drawback was the inability to use all births rather than all breeding years, but the uncertainty in the exactitude of many littersizes and maternal identity would have made more precise calculations less valid. The third problem with this technique is that it sums offspring over each individual mother, which in some cases could give rise to a "pooling fallacy" (Machlis et al. 1985); however, as discussed in Section 5.1.3, the individuals in this study were examined for variability in each measure, and they were found to differ more within an individual mother than between separate mothers. As a result, pooling offspring (and the other measures) was considered a reasonable step, with the qualification that variance was examined before such a move was taken. The data from one particular female, Jenny, were treated slightly differently. This mother appeared somewhat anomalous, in that she produced six litters but failed to rear any of them, seemingly through complete neglect and abandonment within the first week of birth. She therefore had no "within-mother" variation, while she differed greatly from other mothers. As a result, for all of the tests, with the exception of calculating her individual "reproductive success", the data from Jenny were presented as a mean value (e.g. from an average littersize of four).

The results of the "reproductive success" computation gave a slightly different cast to the data, in that females who gave birth to a few successful kittens in a single year were approximately equivalent to those who had large litters over three years with high mortality costs (Table 5.4).

When overall kitten totals, for all mothers, and the Type of Care were tested together, an interesting pattern emerged. A total of 119 kittens were considered (Communal = 72, Solitary = 47), and these were compared for the number of survivors from each of the two Care categories (χ^2= 3.419, df= 1, p= .06; Figure 5.20.c). Although not statistically significant, a trend could be seen, in that more Communal kittens survived proportional to the number born. A second comparison was made, this time separating litters experiencing cooperative care from the other kittens. In this analysis, Communal kittens (e.g. those with two or more mothers, and incorporating their combined litters) and those kittens from litters with one mother and long-term helpers (these helpers were seen to spend much of their time over the pre-weaning period with the litters) were compared

Figure 5.20.a

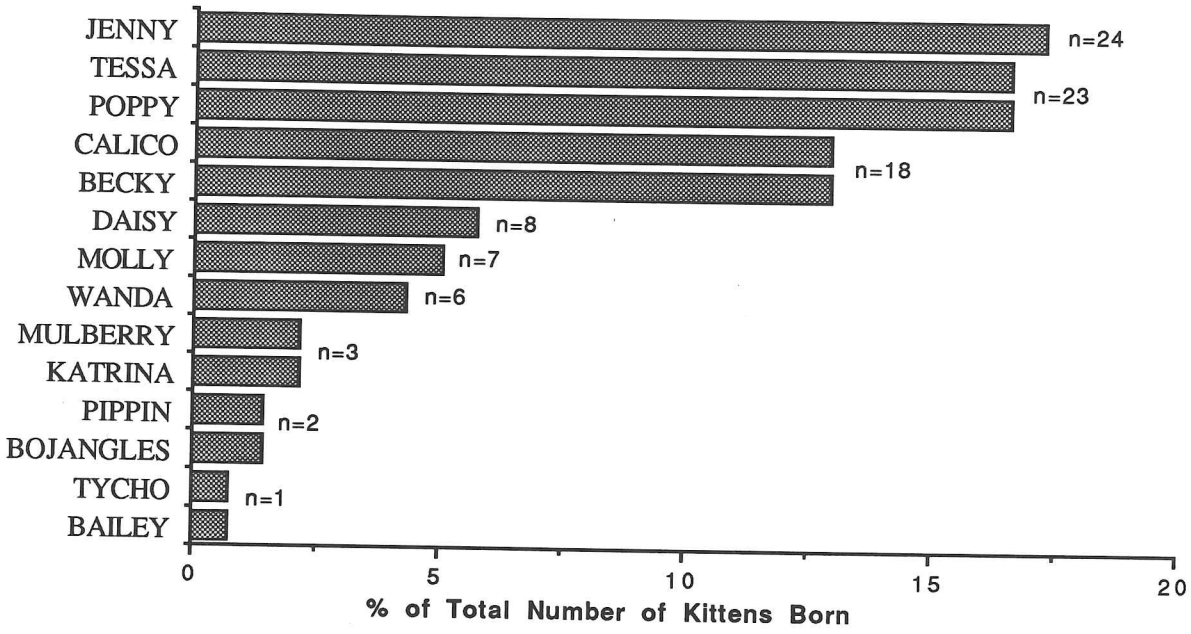

Figure 5.20.b

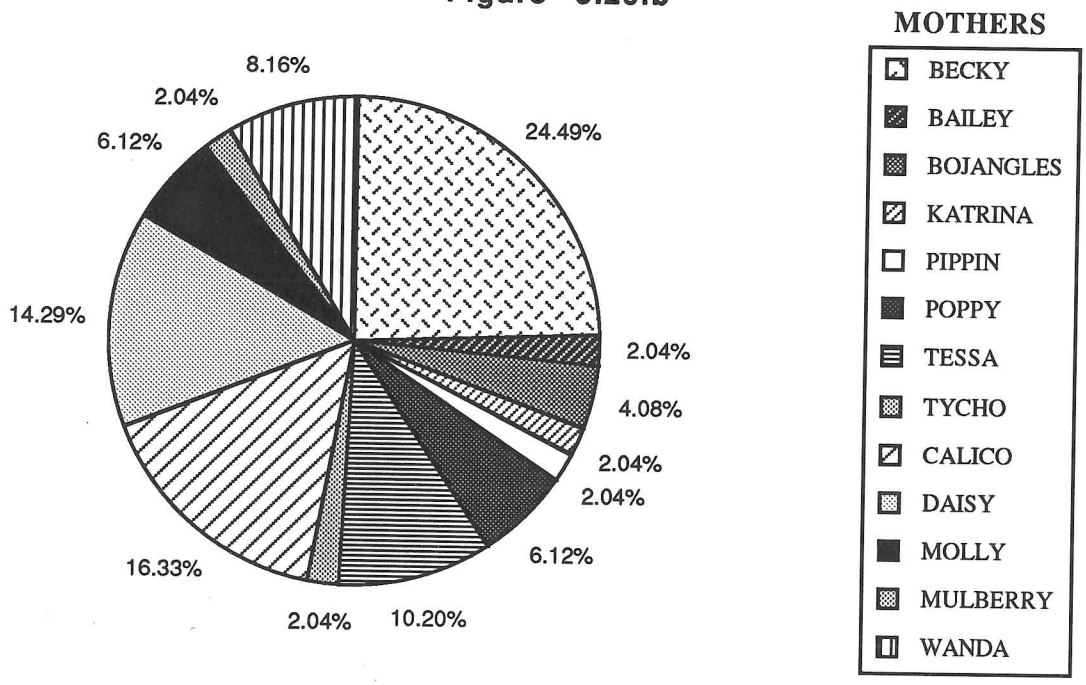

Figure 5.20: Individual mothers and their contributions to the numbers of kittens in the colony. Values are expressed as proportions of the total numbers of kittens in the colony over 1987 to 1989. (a) The proportion of kittens born to each breeding female; (b) The proportion of surviving kittens attributable to each mother.

Figure 5.20.c

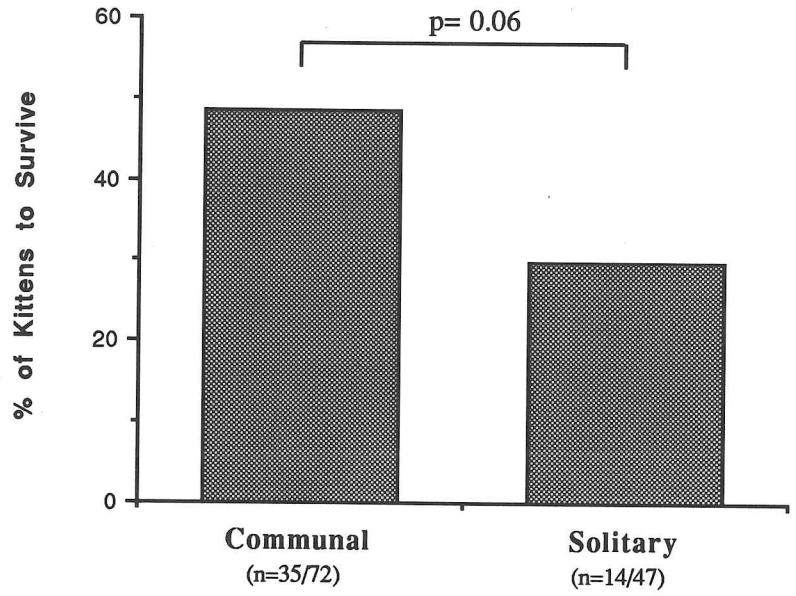

Figure 5.20.d

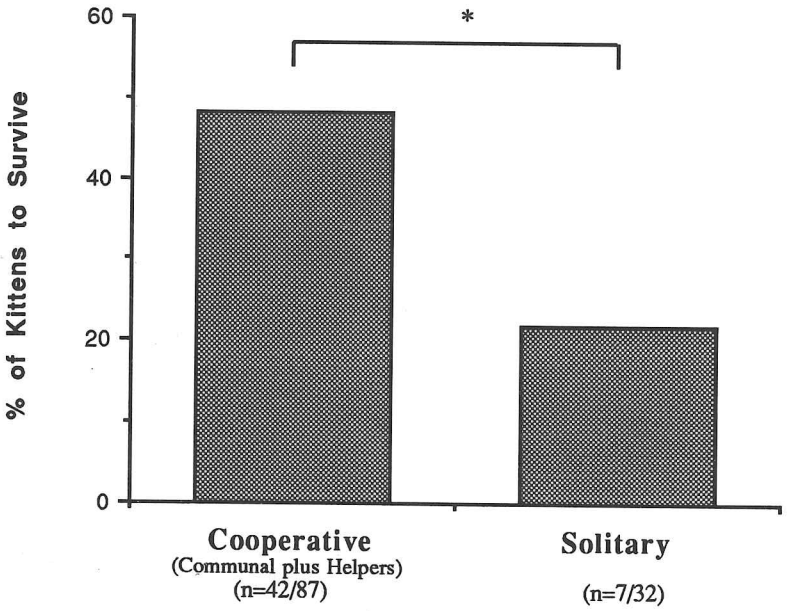

Figure 5.20: The difference in survival (to 4 months) of kittens from Communal and Solitary litters. (**c**) Communal litters versus Solitary ones, where Communal is defined as two or more mothers pooling litters; (**d**) Cooperative litters versus Solitary ones, where Cooperation includes both Communal littera (two or more mothers and combined litters) and those litters with a single mother plus long-term helpers present at the nest. In both of these comparisons, Jenny (a female which abandoned six consecutive Solitary litters) was represented only once (as a mean value), to avoid over-representation of these anomalous data. *$p<0.05$, χ^2-test (2x2 contingency table with Yates correction).

Figure 5.20.e

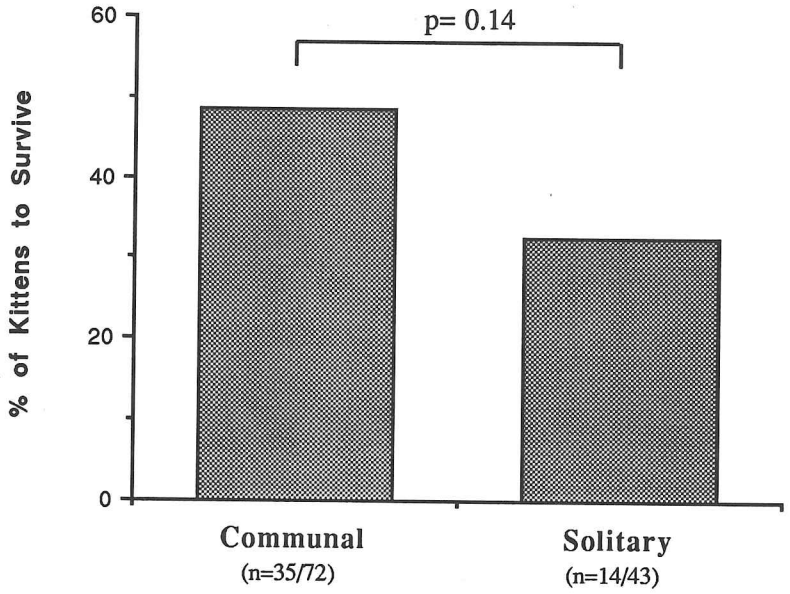

Figure 5.20.f

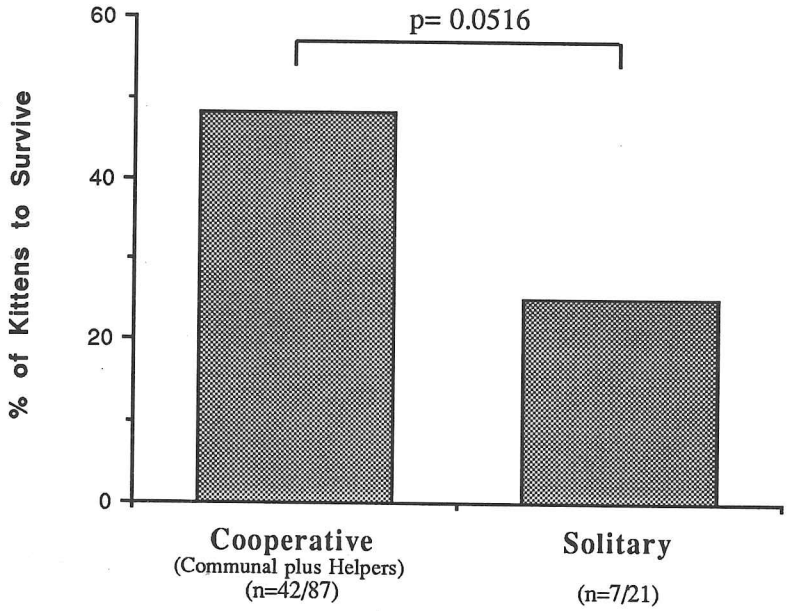

Figure 5.20: The difference in survival (to 4 months) of kittens from Communal and Solitary litters. (e) Communal litters versus Solitary ones, where Communal is defined as two or more mothers pooling litters; (f) Cooperative litters versus Solitary ones, where Cooperation includes both Communal littera (two or more mothers and combined litters) and those litters with a single mother plus long-term helpers present at the nest. In both of these comparisons, Jenny (a female which abandoned six consecutive Solitary litters) was completely removed (compare with Figures 5.20.c and d).

Table 5.4: Individual Mothers and Their Contribution to Post-Weaning Survival

Female Name	Total Survivors	Total Born	% Survival	No. Years Breeding	No. Survivors / Years (="reproductive success")
Becky	12	18	67 %	3	4.0
Bailey	1	1	100 %	1	1.0
Bojangles	2	2	100 %	1	2.0
Katrina	1	3	33 %	1	1.0
Pippin	1	2	50 %	1	1.0
Poppy	3	23	13 %	3	1.0
Tessa	5	23	22 %	3	1.67
Tycho	1	1	100 %	1	1.0
Calico	8	18	44 %	3	2.67
Daisy	7	8	88 %	2	3.5
Jenny	0	24	0 %	3	0
Molly	3	7	43 %	3	1.0
Mulberry	1	3	33 %	1	1.0
Wanda	4	6	67 %	2	2.0

against kittens with only one carer (the mother, "Solitary"). More kittens from these cooperative litters survived than those from the strictly Solitary litters (χ^2= 5.686, df= 1, $p<0.05$; Figure 5.20.d). Thus, in reproductive terms, there would appear to be some benefit to partaking in a communal effort, at least occasionally (if the opportunity presents itself), and a more clear advantage to having help raising kittens (whether from another mother or from cats without current offspring).

As Jenny appeared to be anomalous in her consistent neglect of litters, she was completely removed from the above analyses, and the test statistics were re-calculated to see whether the significant difference (in kitten survival) was an effect of Jenny's presence. When Communal versus Solitary kittens were considered, the difference remained non-significant (χ^2= 2.219, df= 1, p= .14; Figure 5.20.e); in addition, when the Cooperatively-reared kittens were compared to strictly Solitary ones, the effect (of Jenny) was again small, but nudged the significance slightly over the α= 0.05 significance level after the Yates correction factor was applied (χ^2= 3.789, df= 1, p= .0516; Figure 5.20.f). In view of the fact that the test statistic changed very little between the inclusion and removal of Jenny, it is likely that she alone was not responsible for the differences seen in kitten survival; also, considering the consistency of Jenny's behaviour, it is debatable whether it is better to remove her completely from the analysis (versus her inclusion as a mean figure in the earlier tests), as she may well represent one of the possible cases in a more natural setting.

Mean values of each reproductive variable were calculated for each female, and these were used in Spearman Rank Correlations against the proportion of post-weaning survivors per female and the "reproductive success" for each female (Table 5.5). Only five comparisons proved significant: Percent Survival was affected by Date of Birth, such that earlier average births corresponded to higher survival rates; Mother's Age played a role, whereby younger mothers achieved higher kitten survival (undoubtedly due to the fact that several litters of one kitten each were successful - not a surprising result); the number of Nest Sites used in the last three weeks had an unexpected effect, in that fewer nests corresponded to enhanced kitten survival. This was not true of early Nest Sites, which tended to have the opposite relationship. Individual identity was related to the reproductive success measure, i.e. different females had differential success. Increases in Littersize were strongly related to increased "reproductive success", such that large litters resulted in more offspring surviving over time.

Table 5.5: Spearman Correlations Between Mean Reproductive Variables and Two Scores of Offspring Post-Weaning Survival. A significant result indicates that the (ranked) reproductive variable is linearly related to the (ranked) offspring survival measure, e.g. Date-of-Birth and Percent Survival, such that later births had lower survival. Note that careful interpretation of significance levels is required with so many correlations.

X	Y	n	r_s	Z	p	
Date-of-Birth(all)	% Survival	14	-.676	-2.436	<0.05	*
Date-of-Birth(1st)	% Survival	14	-.242	- .873	.38	
Littersize-at-Birth	% Survival	14	-.524	-1.889	.06	
Littersize	% Survival	14	.071	.255	.80	
Mother Age	% Survival	14	-.635	-2.289	<0.05	*
Communal Littersize	% Survival	14	.111	.401	.69	
Budget: Week 1	% Survival	13	-.316	-1.094	.27	
Budget: Week 2	% Survival	13	-.022	- .077	.94	
Budget: Week 3	% Survival	13	-.136	- .470	.64	
Budget: Week 4	% Survival	13	-.512	-1.775	.08	
Budget: Week 5	% Survival	13	-.307	-1.065	.29	
Budget: Week 6	% Survival	12	-.239	- .793	.43	
Budget: Weeks 1-3	% Survival	13	-.260	- .902	.37	
Budget: Weeks 1-6	% Survival	13	-.288	- .998	.32	
Nests Weeks 1-3	% Survival	13	.507	1.756	.08	
Nests Weeks 4-6	% Survival	13	-.571	-1.979	<0.05	*
Nests Weeks 1-6	% Survival	13	.013	.043	.97	
Mother Identity	% Survival	14	.082	.295	.77	
Parity	% Survival	14	-.541	-1.949	.051	
Date-of Birth(all)	"Success"	14	.125	.451	.65	
Date-of-Birth(1st)	"Success"	14	.175	.630	.53	
Littersize-at-Birth	"Success"	14	.423	1.524	.13	
Littersize	"Success"	14	.759	2.735	<0.01	**
Mother Age	"Success"	14	.162	.585	.56	
Communal Littersize	"Success"	14	.276	.994	.32	
Budget: Week 1	"Success"	13	.147	.508	.61	
Budget: Week 2	"Success"	13	.099	.342	.73	
Budget: Week 3	"Success"	13	-.153	- .528	.60	
Budget: Week 4	"Success"	13	-.159	- .549	.58	
Budget: Week 5	"Success"	13	-.078	- .269	.79	
Budget: Week 6	"Success"	12	-.191	- .633	.53	
Budget: Weeks 1-3	"Success"	13	.144	.497	.62	
Budget: Weeks 1-6	"Success"	13	-.200	- .694	.49	
Nests Weeks 1-3	"Success"	13	-.048	- .167	.87	
Nests Weeks 4-6	"Success"	13	-.478	-1.657	.10	
Nests Weeks 1-6	"Success"	13	-.265	- .918	.36	
Mother Identity	"Success"	14	-.667	-2.406	<0.05	*
Parity	"Success"	14	.212	.763	.45	

5.8. SOURCES OF KITTEN MORTALITY

Mortality levels were relatively high in this study, as has been found in other studies on free-living cats (Dards 1979; Kerby 1987). The low incidence of adult mortality was mentioned earlier, and the only cases were due to an undiagnosed pyometra, which ruptured over a non-watch weekend (Katrina), and to incurable mammary tumours in a female beyond breeding age (Laura). Disease was generally confined to the younger animals in the group.

Over the three years of this study, a variety of different factors accounted for kitten mortality, ranging from stillbirth to exposure, and including several disease causes. In 1987, mortality peaked at 78% (similar to the 75% of 1989), and it dropped to a nadir of 54% in 1988; each year, the various factors accounted for a different proportion of the deaths, with exposure/lack of care as the most common contributor. Overall, 139 kittens were born, 95 of which failed to survive (67%); exposure/lack of care resulted in the deaths of 35% of all kittens born, stillbirth took another 13% and cat flu' accounted for 8% (including several "put down" as a result of their condition after infection). "Other causes" accounted for the deaths of 12% of all kittens, and included peritonitis and unknown sources. 7% of all kittens suffered known cannibalism, although the actual cause of death was not ascertainable; it is likely that up to 29% of all kittens were cannibalised, but no remains were left from which to make any diagnoses. Although months 2 to 4 (after birth) have been reported as a time of high wildcat mortality, only 13% of all deaths in this study took place then, and the majority were victims of euthanasia following a severe outbreak of cat flu' in 1989 (it is conceivable that some individuals might have survived in the wild). Figure 5.21.a summarises the causes of kitten mortality, and Figure 5.21.b presents the values pertaining to cannibalism.

Another aspect of mortality included the differential values between kittens of Solitary and Communal mothers. A total of 39 kittens died to Communal mothers (54%), while Solitary mothers lost 56 kittens (84%; including the 6 litters neglected by Jenny). Mortality rates for the different types of care varied year to year, ranging from 22% to 100%, but Solitary mothers always had the higher mortality costs (Table 5.6). Therefore, whether overall mortality or survival past weaning is used as a comparative criterion, there appears to be some increase in maternal "reproductive success" in Communal cats (and particularly when litters with helpers are also included). This has also been seen in other communal species, as reviewed in Harper (1981).

Figure 5.21.a

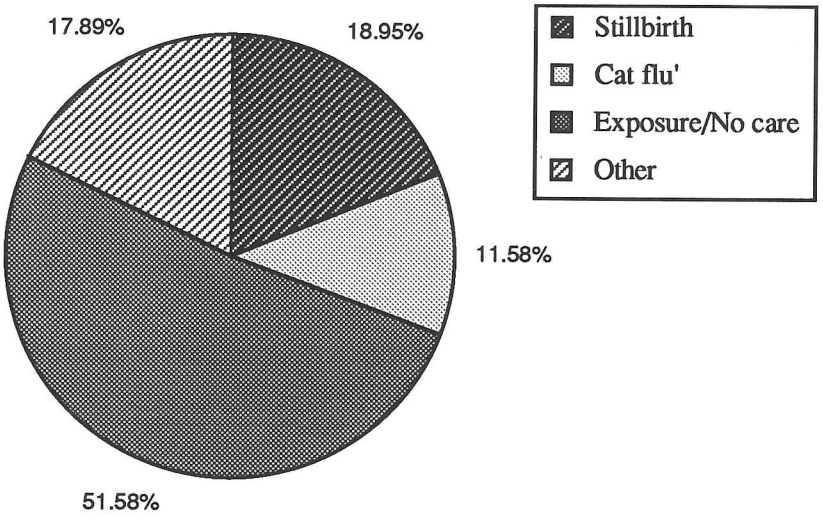

Figure 5.21.b

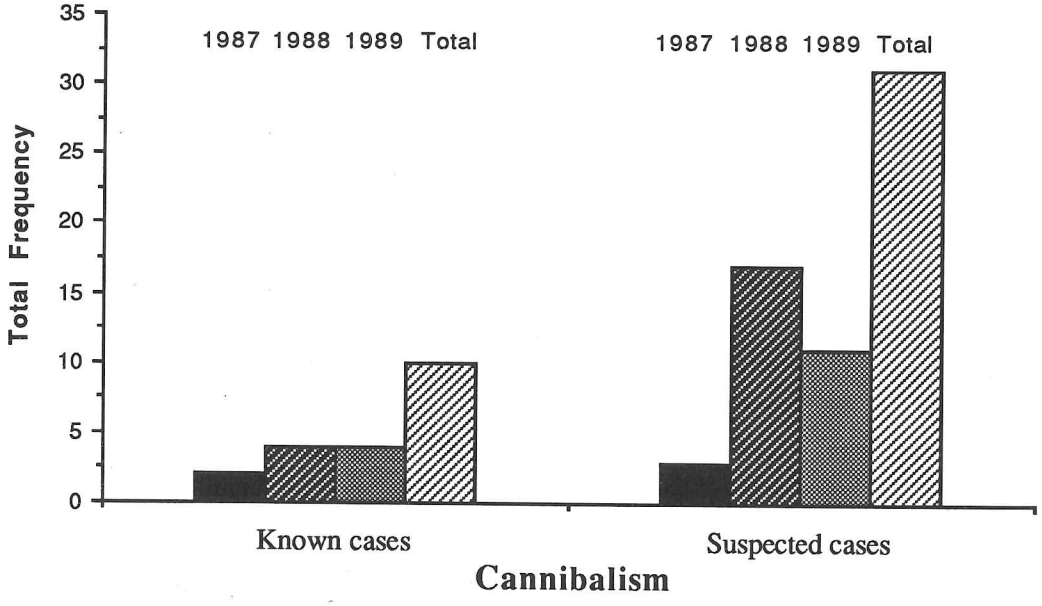

Figure 5.21: Aspects of Kitten Mortality. (**a**) The causes of Kitten Mortality, expressed as percentages of the total number of kitten deaths; (**b**) The frequency of cannibalism of kittens (for "known" cases, remains were found, and for "suspected" cases, the kittens disappeared without a trace).

Table 5.6: The Differences in Kitten Mortality Between Communal and Solitary Females and the Causes of Kitten Deaths

	1987	1988	1989	Total
No. born	41	50	48	139
No. deaths	32	27	36	95
Solitary born	17	31	19	67
Solitary deaths	17	22	17	56
Communal born	24	23	25	72
Communal deaths	15	5	19	39
Stillborn kittens	6	9	3	18
Cat influenza	2	0	9	11
Exposure/No care	16	12	21	49
Other	8	6	3	17
Cannibalised	2	4	4	10
Max. cannibalism	5	21	15	41
Deaths in Months 2 to 4	4	0	8	12

5.9. NEST LOCATION

Apart from the consideration of Nest Site numbers, a second aspect offers additional information: the actual locations of nests. Nest location is reported to be of significance to kitten survival and female reproductive success (Kerby 1987). In the present study, most sites were quite well hidden, incorporating areas of long grass, thistles, nettles or piles of wood; cats also used the wooden huts provided as shelters. As kittens became older and more mobile, nests tended to shift from discrete, covert localities to more open and relatively spread-out areas; a mother might start inside a shelter and later move to the open region underneath or around it. The nests used by each litter were plotted on a diagram of the enclosure (Figures 5.22.a & b). From these illustrations, it is possible to see several trends. Mothers appear to use certain locations preferentially, as shown by the repeated use of the huts, and older litters are generally moved toward the feeding site.

The same females were seen to use a single nest several times for one litter, or for multiple litters; different females used the same site (at separate times, unless Communal). There was no paucity of suitable nesting places, but it is possible that the wooden shelters were deemed preferable places for young kittens, as they were the most weather-resistant. With this in mind, however, some huts went unoccupied while other places were used, so it is unlikely that they were a limited resource subject to competition. The occupation of huts during early kitten development did not appear to affect kitten survival, and, as mentioned in Chapter 2, the number of huts should neither have limited nest choice nor have been a welfare problem. When kittens raised in a hut for at least part of the first week were compared to kittens raised outside only, no difference was seen in kitten survival (χ^2= .347, df= 1, p= .56). Furthermore, when litters raised in a hut only were compared with litters raised outside (some or all of the time), the difference remained non-significant (χ^2= .356, df= 1, p= .55). When nest location in the first week was compared over all litters, including inside only, outside only and both types of location, no difference was seen in litter mortality using a Kruskal-Wallis test (H= .564, df= 2, n= 27, p= .75). The first week after birth was the most sensitive period in terms of thermoregulation, and was the time of least nest-moves, however, even at this crucial stage, nesting inside or outside a hut made no difference to kitten survival. In addition, weather seemed to have little effect on kitten mortality over the first six weeks (or up to four months) (Mean Maximum Temperature: r_s= .441, Z= 1.82, p= .07, n= 18; Mean Minimum Temperature: r_s= .399, Z= 1.644, p= .10, n= 18; Hours of Sun: r_s= .41, Z= 1.692, p= .09, n= 18; Rainfall: r_s= .137, Z= .564, p= .57, n= 18), calculated from the date of birth and the weather during the early weeks of kitten development. Location may, to some extent, have been a matter of individual preference, or it may have depended upon

SIDE A - TROSSACHS

NEST SITES: 1987-1989

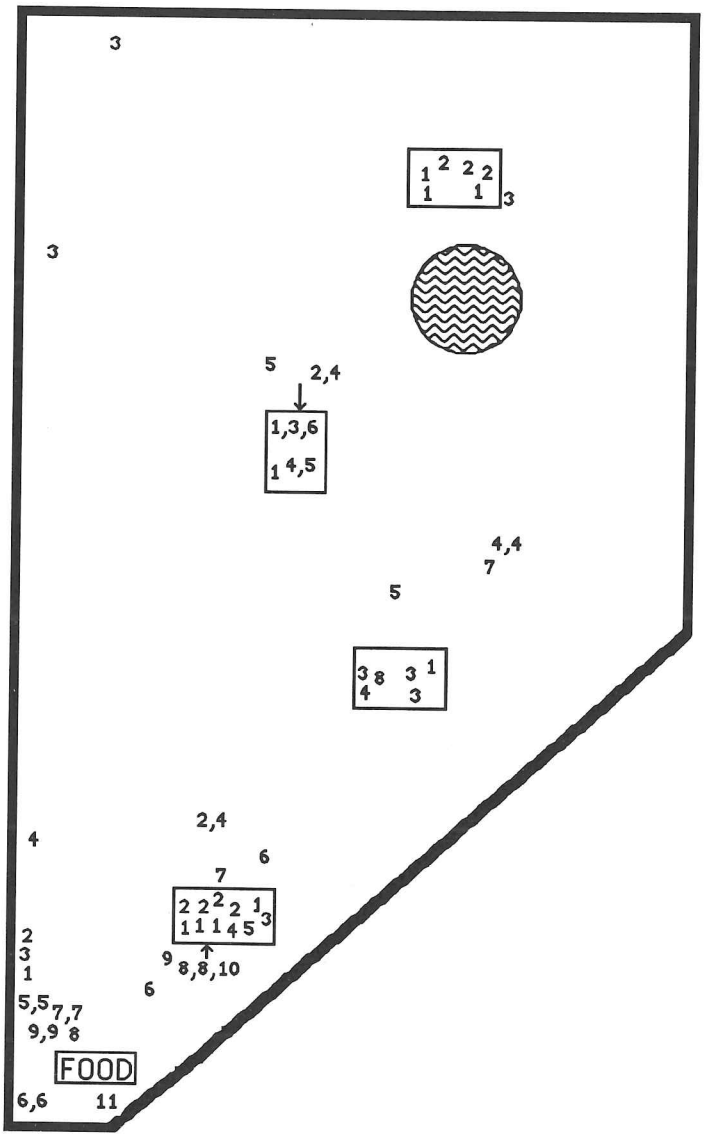

Figure 5.22.a: Location of Nest Sites in Group A. Boxes indicate wooden shelters, and the general feeding area is indicated. Numbers represent the number of the nest site (cumulative for each litter); where communal, nests are separated by commas.

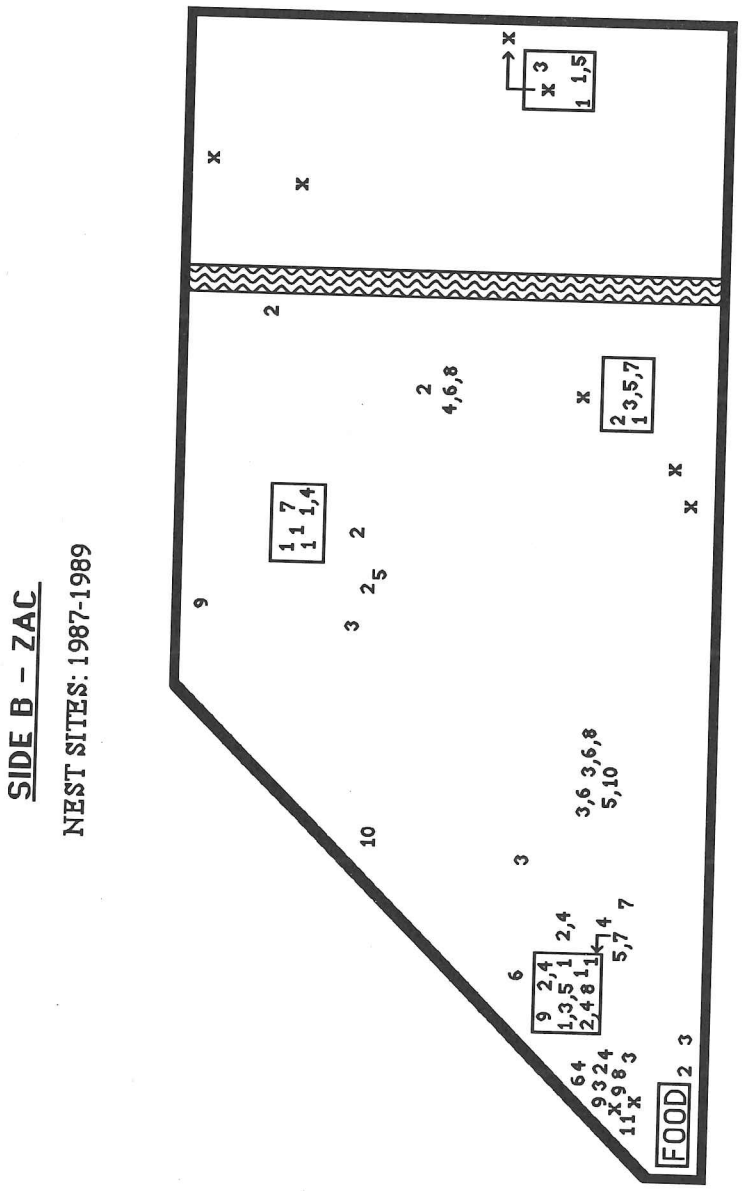

Figure 5.22.b: Location of Nest Sites in Group B. Boxes indicate wooden shelters. Numbers represent the number of the nest site (cumulative for each litter), and communal litters are separated by commas. "X" marks the locations of abandoned kittens (e.g. stillborn, or left at birth but still alive).

concurrent mothers and their nest sites. A female may have avoided adjoining nests or preferentially initiated a late pooling of kittens.

Overall, it would appear that kittens are gradually moved closer to a food source as they develop. In the enclosure, the primary source of food was a single site for each group, supplemented by maternal provision of prey, so that directional changes were more apparent. It would seem that, to facilitate the weaning process, females may deliberately introduce kittens into the environs of solid food. When around the age of eating solids, kittens are still small and somewhat unsteady on their legs; most nest locations would require a long journey through thick undergrowth, past unfamiliar conspecifics, both there and back. Habitual paths would help the location of food, but only if a kitten was on the right path, in the right direction; at what age do kittens recognise the social significance of well-worn trails?

Several possible scenarios account for the observed patterns: kittens born into outlying nests are moved toward the central food area; or kittens born near the food site remain in the region, with the possibility of a brief move to nether parts. This explains the scattering of early nests in the food locale.

Therefore, it would seem that females have specific reasons for choosing any particular nest location; these are thought to include the following aspects: the degree of cover, for protection from weather and prying eyes; the proximity to food sources for weaning kittens; and possibly the social surroundings, depending on the nest sites of other mothers.

5.10. DISCUSSION

In summary, this chapter has investigated the interactions between various reproductive factors. The first part of the analysis examined the two groups of females, from Side A and Side B of the study enclosure, to ask whether the data from all females could be pooled. None of the following variables were found to be significantly different, including: Date of Birth, Littersize-at-Birth, Littersize, Communal Littersize, Maternal Time Budget, Kitten Mortality, Parity, or Mother's Age. Group A females used more Nest Sites in the first three weeks after parturition, but this was probably an effect of the Type of Care (as a greater proportion of Group A females were Communal). As a result of the analysis, all the females were combined for subsequent tests of reproductive variables. Other findings from the consideration of the two groups included the fact that most females had only one or two litters each year, and that spring oestrus and parturition were relatively synchronised. Second litters invariably failed before reaching weaning age.

The second section of the chapter examined Primiparous and Multiparous females to ask if maternal experience had any effect on reproductive measures. Surprisingly few differences were found between the inexperienced and experienced mothers; Date of Birth, Littersize, Communal Littersize, Maternal Time Budget, Kitten Mortality and Nest Sites all showed non-significant differences. Primiparous females were typically younger than Multiparous mothers, which simply reflects the fact that they were involved in their first litters rather than later ones. Primiparous mothers also gave birth to significantly smaller litters (Littersize-at-Birth), a point which is commonly reported (Scott 1976; Deag et al. 1988). Multiparous mothers may spend slightly less time with their litters, when mean Time Budget was considered, but the effect was not strong. When all mothers were included in the analysis, Multiparas had higher Kitten Mortality; however, this effect disappeared when a single Multiparous female was excluded due to the failure of all six of her litters. In this study, most Primiparas were Communal mothers. Also, different levels within "multiparous", accounting for the exact number of litters for each experienced mother, did not have significant differences for any variable.

The third section investigated the two types of maternal care, and inquired if Communal litters (and mothers) were significantly different from those litters raised by Solitary mothers. Communal litters were born earlier in the year, and one explanation is that litters born synchronously (e.g. in the first peak of spring births) were more likely to be Communal due to the presence of other new litters. This still did not explain the phenomenon of litters pooled some weeks after birth (or those of widely disparate age), but may have explained some of the Communal litters. Communal and Solitary litters had similar Littersizes-at-Birth, but Communal litters had greater Littersizes once early mortality was considered; this difference was due to a Solitary female and her litter failures, and no difference was found once this particular individual was removed from the analysis. Communal Littersize (after pooling) was significantly larger than the size of single (Solitary) litters. Solitary and Communal mothers spent similar amounts of time (Maternal Time Budget) with their litters, although Communal litters may have been with a female more of the time than Solitary litters (e.g. due to overlap of multiple mothers). Communal litters had less Kitten Mortality than Solitary litters, but the difference was only significant when all litters (including those which failed within a day of birth, and therefore received little classifiable care) were included. Also, larger litters suffered lower proportionate mortality. Communal litters were reared in twice as many Nest Sites as Solitary litters, particularly during the first three weeks after birth. It was not possible to test whether Primiparous females or Communal females had a stronger effect on the significant variables.

The fourth section looked at individual variation in reproductive variables, both to ask whether this was a large effect, and also to investigate some potential sources of

the differences from earlier sections. The same females often showed both Solitary and Communal care for separate litters. The within-female variation was larger than the between-female differences for Maternal Time Budget, Kitten Mortality, and Nest Sites; therefore, disparities between Primiparas versus Multiparas and Solitary versus Communal females were probably not due to any one female's contribution. Parity and Mother's Age did vary among the females, due to the presence of young breeding individuals born during the study. A few anecdotes were discussed regarding the phenomenon of helping, as well as sharing communally; helpers included females (both nulliparous and non-breeding, kin and non-kin) as well as young males (mainly kin, although not always). Helpers spent less time with the litters, and the affected litters were termed "cooperative" rather than "communal" (where two females appeared to contribute more equally). Communal mothers spent approximately similar amounts of time with the litter, although some exceptions were seen.

Kitten development was examined, in the fifth section, to ask whether differences in reproductive variables were related to changes in the speed of development. None of the following variables had any effect: the identity of the mother; Date of Birth; Parity; Littersize; Communal Littersize; nor Maternal Time Budget. Communal kittens left their nests significantly earlier than Solitary kittens, and this may have been related to the number of Nests occupied in the last three weeks (of a six-week period after birth). The rate of development did not affect Kitten Mortality.

In Section 5.7, a measure of "reproductive success" was derived (Kerby 1987) from those kittens who survived to the age of four months. Different mothers engendered different numbers of kittens, and these survived at different levels, giving a range of individual "reproductive success" scores (0-4). Earlier average Dates of Birth corresponded to higher rates of kitten survival, as did younger mothers (probably due to small litters), more early Nest Sites, fewer later Nest Sites, and larger Littersizes. Somewhat more Communal kittens survived than did Solitary kittens (non-significant), while more kittens from litters with helpers as well as those with multiple mother-carers survived than those with a single Solitary mother, suggesting a clear advantage to cooperative care from an evolutionary viewpoint. (However, the probability levels were reduced slightly, but not drastically, when the anomalous female, Jenny, was excluded from the analysis.)

The penultimate part of the chapter specified the sources of kitten mortality, in that 54-78% of all kittens born each year died. Exposure or lack of care was the single largest cause of death, followed by stillbirth, unknown reasons (including most disease), and then cat influenza. Cannibalism was seen to affect at least 7% of all kittens born, and this was a minimum value. More Solitary kittens died each year than did Communal kittens.

The last section discussed the location of nest sites, and looked for a pattern in the placement of nests. Most litters were moved during the first six weeks after birth, some nests were used repeatedly by the same female (for one or more litters) and by several different females (for shared or separate litters). Many potential sites were rarely or never used. As kittens approached weaning age, their nest locations approached the food source. Females appear to choose specific nest sites, and factors may include the degree of shelter, the location of food sources, and perhaps the proximity of other females.

The results of the analysis on maternal reproductive variables provide a number of interesting answers, and beg still more questions. Overall, no differences were found between the two groups of females for any notable reproductive variable; this was a logical result, as the cats came from a similar (if not identical) previous background, were selected for their maternal prowess, and were then subjected to consistent conditions. Weather, food provisioning, and habitat were all factors that provided little source of variability for the two groups. The slight disparities which were found included the larger Communal Littersize and more early Nest Sites in Side A; the difference in Communal Littersize was probably due to the tendency in one particularly Communal female toward large litters (and therefore represents an aspect of individual variation). The Nest Site difference was an indirect result of the Type of Care, and was not a direct result of the grouping. Several adult females did not breed during the study, and of those that did, at least one mother failed to rear any kittens successfully (also reported by Kerby 1987). Any second litters born in a given year were unsuccessful, and kittens failed to survive past the first six weeks (also seen by Kerby 1987). Because of the lack of differences between the two groups, Sides A and B were pooled for all further analyses.

There were some differences between Primiparous and Multiparous mothers, but fewer than might have been expected if one conjectured that experience serves to refine technique and enhance efficiency. First-time mothers were younger and tended to produce smaller litters, as noted in other studies (Deag et al. 1988); there was an indication that inexperienced females spent more time with their kittens, but this effect was confounded by the fact that five of the seven Primiparas were Communal (four of these pooled kittens together). Experienced mothers should be less likely to waste energy by over-investing in offspring (Harper 1981). A study by Deag, Manning and Lawrence (1988) found no effect of parity on kitten growth or mother weight, supporting the fact that there was no significant difference in Maternal Time Budgets (used as a rough measure of reproductive effort) for the cats examined here. As was discussed briefly at the end of Section 5.3.6, little disparity was seen between the maternal actions displayed by experienced and inexperienced females; apparently, inexperience had no detrimental effect.

This contrasts with any studies in which Primiparas suffered a uniform lack of success in litter-rearing (e.g. Kerby 1987).

One possibility is that the case is as stated: there is no difference, except that Primiparas are liable to have much smaller litters (probably a physiological constraint rather than a way of minimising losses, as mortality was not dependent on previous experience). The induction of maternal behaviour may be a further explanation for the lack of differences between Primiparous and Multiparous females (Caro & Bateson 1986); a female may have the underlying structure for the expression of full maternal behaviour, but contact with kittens prior to breeding might facilitate the onset of such actions. (This differs from the following explanation in that specific opportunities for practice of the behaviour are not required, as for learning, but merely trigger appropriate activities.) A third possibility is that several of the Primiparas played a helping role prior to their own parturition, and this early experience honed their maternal skills. In this scenario, a completely inexperienced female would suffer some cost, either in her own output of effort or in the form of offspring mortality, which could be minimised by learning through helping. The last situation invokes the benefits of cooperative rearing of kittens; a young mother might minimise her deleterious effects on her offspring by combining them with the kittens of another female, possibly one with more experience, but not necessarily. (It is difficult to think how a female might assess the previous reproductive skills of a companion, especially if she herself is young enough to be breeding for the first time, unless the companion is her own mother or allomother.) The latter two explanations pivot on the existence of cooperative rearing as a viable reproductive strategy in cats. It is therefore necessary to examine the dual strategies of Solitary and Communal care, as evidenced by the cats in the study.

Communal litters were typically formed by mothers who gave birth close in time. It is impossible to rule out the possibility that the pooling of kittens was a circumstantial effect of synchrony; however, there were several instances of cooperation between mothers with kittens of hugely disparate age (e.g. Wanda and Calico, 6 weeks). In these cases, kittens that were almost completely weaned were combined in nests with neonates; both the new mother, and the mother who would typically have been finishing with lactation, were seen to nurse kittens, both old and young. Surely, unless there was a more directed force guiding the interaction, the lack of timing synchrony would have forestalled such an eventuality.

Whatever the immediate cause for Communal care, it is still possible to examine the differences between that and Solitary care. Communal litters tended to be larger (after pooling) than Solitary ones. Communal mothers spent about the same amount of time with the kittens as did Solitary mothers, so no apparent benefit accrued through a reduction in effort spread across several cats; a similar mortality rate was found for those

Solitary and Communal litters that received any care (although, overall, more "Solitary" kittens suffered mortality). As speculated in Section 5.4, if a single female severely neglects her litter, without the aid of helpers or other mothers, the kittens cannot survive (especially in the first three weeks); however, if this "poor" mother were to give birth in a communal nest or moved her neonates to such a site shortly after birth, there would be a greater chance of survival due to the potential ministrations of an allomother. It is at this stage that the relationships between females come into effect: if the two mothers have a generally amicable relationship, there will be more mutual tolerance in the nest; if, on the other hand, the mothers are generally agonistic or lack reinforcing social bonds, a chance persists that nest-sharing will not be allowed. A graphic example of the latter is the case of Poppy and Tessa, 1989 (detailed in Section 5.5.5), which resulted in the mass mortality of all eleven Communal kittens.

A further difference between Communal and Solitary litters was shown when Nest Sites were examined. Communal kittens were found to occupy twice as many nests, particularly during the first three weeks. Several hypotheses can be presented to explain the common observation that cats move their litters over the pre-weaning period; the first is that the nests accumulate ectoparasites and become contaminated by elimination products, so that mothers move the litters to decrease the chances of disease (Corbett 1979; Deag et al. 1988). Common sense would then explain the frequent nest moves in Communal mothers by the acceleration of contamination with larger litters; however, several points counter this argument. Combined litters are often surprisingly small (minimum=2), although the larger ones are more notable, and can be smaller than adjoining Solitary litters; furthermore, despite an unlimited number of possible sites, females often used the same ones several times, even within a few days. A third aspect is the fact that mother cats stimulate urination and defaecation in young kittens, and then consume the products, presumably to keep the nest clean and to remove odour that might attract predators; so, especially in the first three weeks (Ewer 1973), contamination by elimination should not be a feature. (Whereas, in the latter three weeks, when kittens are starting to eat solids and to control their own elimination processes, nests might be much more prone to becoming dirty; this is not the key period when there was a difference seen between the two groups.) Other authors have noted that cats (e.g. cheetah) are known, in some cases, to change nest location so frequently that it is less likely that the nests are unsuitable (e.g. due to unhygienic conditions) and more possible that the moves are a protective measure against predators and potentially hostile conspecifics (see below); this was also noted in a canid species, the golden jackal (Ewer 1973)

A second hypothesis regarding Nest Sites is that females move kittens as a result of being disturbed. It is more difficult to rule out this possibility, as the constant peregrinations of non-kitten companions may prompt the need for frequent changes (and

especially if that companion invokes a tense atmosphere to the nest). However, the common sight of both (or all) allomothers and/or helpers mutually moving kittens to a new nest may indicate that this is not the whole answer.

A third explanation harks back to one of the postulated reasons for having nests at all. It is speculated that the use of secluded, well-hidden sites may minimise the dangers of discovery by predators or strange conspecifics. Most small cats are seen to use similarly covert locations, with a dearth of "nest-building" actions (Corbett 1979; Fitzgerald & Karl 1986); predators are common, and pose a particular threat to an unprotected nest when the mother is out hunting. Frequent changes of location would maintain concealment, as would infrequent maternal visits. During the lactation period, kittens suckle relatively often, and the mother is generally present except for short forays (hungry kittens make constant, obvious piercing sounds, sure to guide any danger to the door); when the kittens grow older, and solid food is introduced, the mother can return less often and may spend longer periods away hunting. In the first few weeks of dependence, several females can more efficiently transport a litter, without increasing kitten vulnerability, than can a Solitary mother; perhaps the doubled number of nests in Communal litters indicates a greater freedom to relocate than is found in single-carer litters. However, the possibility remains that the increased comings-and-goings of multiple cats can draw attention to the nest site, and moving is just a way to compensate for this detrimental by-product of communality.

A potential cost of Communal litters has been mentioned by several authors (Deag et al. 1988); disease may be more easily transmitted in a combined nest, and kittens which fail to suckle the colostrum from their mother shortly after birth may have weak immunity. From the cats observed in this study, a large proportion of litters were combined at birth, supplying two or more mothers able to provide colostrum; more disparate litters were always seen to primarily suckle from their own mothers in the first two weeks or so. It is unlikely that the provision of passive immunity through colostrum was absent in Communal litters, as supported by the fact that they appeared no more liable to suffer disease or early mortality. The transmission of disease within Communal litters is more difficult to refute; overall, the two mothering styles incurred no differential mortality, although disease was present. However, there was one instance when cat flu' was distributed throughout a Communal litter, resulting in widespread mortality; in this case, all young cats in the group, whether Communal or Solitary, including much older individuals, were affected, due to interactions through curiosity, helping and play. In general, from the results of this study, it seems that the potential costs through disease transmission are outweighed by benefits sufficient to keep cooperative rearing in the behavioural repertoire.

Overall, as was presented in Sections 5.7 and 5.8, Communal litters produced more surviving juveniles, especially when litters with helpers were included; this

would appear to be a clear benefit of pooled efforts, although it was not obvious at the level of individual litter mortality. It may be that cooperative (and particularly Communal) care provides a selective advantage in the long-term, but not for any single breeding attempt. Therefore, as long as a female takes any cooperative opportunities provided, she will enhance her lifetime reproductive output without needing to adhere to the same strategy with every litter. Nulliparous individuals might also be provided with a learning experience through helping, whether or not this aids the helper immediately. This might assist in explaining the observed presence of both Solitary and Communal strategies, and the variation between different populations. There was no clear detriment to being Solitary (in the sense of being a "single mother"), and this maternal style will persist whether it is an hereditary method or just the consequence of isolated births; Communal litters leave slightly more offspring, so may increase the likelihood of cooperation in subsequent generations (if the tendency is genetic), or may provide the learning ground for surrounding individuals, or it might just be the beneficial by-product of oestrus synchronisation (which in turn might minimise inter-male aggression, and stabilise groups).

The following chapter (Chapter 6) integrates the previous chapters, dealing with social behaviour, with the results of this reproductive analysis in an attempt to explain the affiliative sociality and cooperative rearing of kittens seen in cat groups.

A communal litter (n=11) belonging to Becky (seen nursing 10 kittens) and Tessa (watching).(see Chapter 5)

Chapter 6

Sociality and Its Relationship With Reproductive Systems

Previous studies of the domestic cat, in its various forms from farm cat to feral animal, have put their findings into the context of mammalian ecology, and particularly the concepts pertaining to carnivore sociality (Corbett 1979; Dards 1979; Liberg 1981; Panaman 1981; Kerby 1987; Macdonald et al. 1987). It seems well-established that the distribution and abundance of necessary resources act as the organising feature for animal populations (Macdonald 1983), and the cat is also considered in this light. Without sufficient supplies of limiting resources, groups cannot form and stabilise; the necessary intra-specific competition for survival would preclude concentrations of animals in small areas. If a predictable and abundant food source is taken as the starting point for group formation, along with adequate shelter, then aggregations of cats can be explained. However, animals can share clumped resources without necessitating affiliative relationships, and it is these social associations which call for further elucidation. Several authors (Macdonald & Apps 1978; Dards 1979; Panaman 1981; Kerby 1987; Macdonald et al. 1987; Ohkawa & Hidaka 1987) have indicated a tendency for communal rearing of kittens in cat groups, and they then suggest that the potential benefits of cooperation may play a role in explaining the evolution of socially cohesive populations.

Few cat groups offer the opportunity to study both general social behaviour and the details of reproduction, due to the tendency for female cats to rear their offspring in well-hidden and secluded dens or nests. Only through enclosing the cats could behaviour and reproduction be examined together in this study, although the attendant cost was the lack of free movement in and out of the group; activities such as predation and interactions with intruders were seldom evinced and could not be studied in depth. Nor could home ranges, or even the large-scale proximity relationships, be fully understood. Instead, this study sought to disclose the reproductive actions of female cats, especially the phenomenon of cooperative care. Social relationships between the constituent members of the two study groups were described in order to explain the affiliations seen during breeding. The underlying proximate hypothesis was that affiliative relationships were the active bonding ingredient predisposing cats to cooperate; in other words, in a cat group with strong amicable associations, cooperation is a predictable outcome of individual relationships, and indeed may ultimately be one selected trait involved in maintaining social aggregations.

The social organisation of each of two cat groups involved in this study was investigated through the spatial and behavioural relationships within the groups. Some of the results supported previous studies, while other aspects were more characteristic to the conditions of this population. Both proximity and behavioural interactions were non-random, in that individual cats spent differing proportions of time near other cats (Chapter 3) and had varying rates of each pattern of behaviour and for overall behavioural totals

(Chapter 4); each individual directed more interactions toward specific others, and demonstrated a predilection for certain partners when initiating actions (Macdonald & Apps 1978; Kerby 1987; Macdonald et al. 1987; Kerby & Macdonald 1988). Males and Females differed in their spatial relationships, as did Adults, Juveniles and Kittens; however, no overall differences were found between the two study groups with respect to spatial relationships, for any age class (Chapter 3). Females appeared to be the basis upon which group sociality was founded, and tended to aggregate together within the available space, along with the other Females (both Adults and Juveniles). Females who cooperated together during the study were particularly closely associated in terms of spatial relationships. Juveniles often formed a separate cluster within the group (Panaman 1981) and associated among themselves, as well as with both Adults and Kittens. Based upon the observed relationships, it seems possible that Adult-Juvenile proximity interactions may be directed by certain factors, including kinship (e.g. mother-offspring), early social experience (e.g. allomothers and helpers), as well as by group features (e.g. inter-Male conflict, reproduction) and individual variation. Males were seldom seen close to other cats (Macdonald et al. 1987), particularly other Males, and yet they were often the subject of social behaviour initiated by Females (as seen in Chapter 4). Proximities less than thirty centimetres appeared to be the most sensitive to specific social relationships, while distances greater than one metre seemed to reflect more general associations.

The results of the investigation of spatial associations were supported and supplemented by information regarding the specific behavioural interactions between group members (Chapter 4). As with proximity, no major differences were found between the two study groups (regarding social behaviour) for Adults. More interactions were exchanged between Adult Females than for any other combination of cats, and these activities were primarily amicable, including the initiation of contact (e.g. Pawing, Rubbing and Grooming). Male-Female interactions were of varying nature, predominantly acting as part of the mating process (Kerby 1987), although Females did direct some affiliative activities to Males (Dards 1979; Macdonald et al. 1987); certain combinations of Male and Female individuals showed more amicable encounters, while other Females appeared to have little connection with Males outside of mating (Panaman 1981). Males were rarely the initiators of affiliative behaviour to others, including Females, Juveniles and Kittens, while they were more often the recipients of the affiliative attentions of such others. The interactions between Males and Juveniles were primarily in the course of investigation (e.g. Approach and Sniffing), with the addition of agonistic acts to other Males (Corbett 1979; Dards 1979; Kerby 1987) and reproductive interest in young Females.

Juveniles appeared to interact most amiably with their littermates, both related and communal cats (Dards 1979), as well as with their mothers and more "familiar"

Females (e.g. "aunts" or allomothers). These relationships were overlain by other considerations, such as mating. Juveniles were often with much younger cats, the Kittens, and exchanges were reciprocal in that the degree of initiation was related to the level of receiving; cats who showed great interest in Kittens in the form of directed behaviour were also the common recipients of Kitten initiations. Agonism was rarely seen to involve Kittens, either as initiators or as recipients (Dards 1979); sometimes the Adult and Juvenile Males avoided Kittens, and Females occasionally Swiped Kittens, but no serious aggression was recorded. Adult Females also displayed relatively high levels of maternal behaviour toward Kittens, including Nursing, Grooming and Playing, along with generally Resting in Contact with the young cats (Dards 1979; Panaman 1981; Macdonald et al. 1987).

All the observations were complicated by the presence of individual differences in behaviour. One of the problems with studying cat populations with regard to ecological factors is the high degree of variation among members of this species. This may obscure trends when all group members are included for larger populations, and smaller populations may show only the characteristics of the particular members under investigation, rather than more general patterns. In the present study, all Females displayed some variation in the behaviour initiated to other cats, both in type and in rate; this included maternal actions to Kittens. Overall, few differences were seen between activities directed to a Female's own Kittens versus those offspring of other mothers (Macdonald & Apps 1978; Dards 1979; Macdonald et al. 1987); however, several individuals showed strong "preferences" for their own Kittens.

Males also differed in behaviour rates, but despite these variations, they were generally the net initiators for agonistic and mating behaviour, they performed many of the vocalisations, and received a large number of the total Hisses and Growls. Only some of the Males were observed to copulate successfully with Females, although all Males were seen in Mount attempts; no Male-Male aggression was shown in the context of mating access, and multiple Males were often seen around Females in oestrus (Natoli 1990). However, in such cases, only the Adult Male (e.g. Zac) was observed to Mount; younger Males Mounted less often in the presence of the Adult, although he was seen to approach while other Males were thus engaged with little result. Juveniles displayed quite high levels of individual variation in behaviour rates, and Females were generally more affiliative than Males. Altogether, Juveniles also contributed much of the Object Play and considerably less of the vocalising than did Adults. Juveniles were also observed engaged in Mounting inappropriate subjects (especially Kittens and other Male Juveniles), although Adults occasionally did the same (Michael 1961; Dards 1979; Kerby 1987).

The variations in individual behaviour probably had some effect on the dyadic exchanges, which also showed large differences. Only Adult-Adult dyads were

tested for asymmetry, and the results indicated a strong directional component to many combinations of cats and activities (e.g. Grooming; Macdonald & Apps 1978). These imbalances included affiliative acts by Females to Males, as well as differences in cooperating Females; pairs of Females sometimes had mutual initiations of affiliative behaviour, while others demonstrated a dichotomy in that one Female consistently directed to another with little reciprocation of such behaviour.

Overall, contact or affiliative behaviour was the most common, followed by vocalisations; agonism, and particularly serious aggression, was fairly rare. Occasionally Male-Male Fights were seen to spark off Female Fights, perhaps due to increased tension among the cats (Dards 1979); the sound of fighting appeared to make all the cats agitated and restless, and had different effects on the two groups. Cats in the adjoining group often reacted with small outbursts of agonism among themselves (especially one Female, Tessa, who consistently struck out at nearby cats when a Fight was heard), while cats within the fighting group either scattered (Juvenile Males) or ran toward the fighters and "attacked" them (Adult Females). The differences in response probably stem from varying pressures on the age and sex classes; young Males are commonly the recipients of aggression and seem to act so as to avoid conflict, while Adult Females appear to try to separate or subdue fighting Males (also seen in primates: Datta 1983). Perhaps this is due to their tendency to guard Kittens from strange Males; a Fight may be a good indicator of intruders, and Females may behave in a way that helps deter these incursions. Or the Females may be protecting their maturing Male offspring from the aggression of older Males, although this is less likely unless the vocalisations allow identification of the fighters (as Females respond instantly to an encounter, most of which are out-of-sight).

Females were rarely seen to Spray-Mark in this study, although Males did so commonly (also in Macdonald & Apps 1978; Dards 1979; Kerby & Macdonald 1988); again, individuals differed in the rate of Urine-Spraying, from 2.8 Sprays (Zac) to 9.2 Sprays (Trossachs) per observation hour, rates similar to those seen in the study by Corbett (1979). It is possible that this variation reflects either differences in "status" or "territoriality". Certainly, Trossachs actively seemed to patrol along the perimeter adjoining the other group, while Zac did so rarely. However, several of Zac's sons were more involved (than Zac) in patrolling and pacing the dividing fence as they matured, again apparently indicating some individual variation in "territorial"-type activities. The Scratching of trees held little support for the concept of a territory defined along its perimeters, as most Scratching took place along paths (as with Sprays in Panaman 1981); most Scratching involved trees that had softer bark, which yielded more readily to claws (for sharpening?) and left clearly discernible patches (as Marks?).

A rather cursory examination of elimination patterns was made; cats tended to defaecate outside of the central feeding area (greater than ten metres away) while they urinated somewhat more often within this range. As an overall total, most elimination occurred well away from the "core" region, especially in the case of Males. About one-third of all faeces were left completely exposed (Corbett 1979; Liberg 1980; Panaman 1981), and cats often left these deposits without sniffing them (Macdonald et al. 1987), as has been suggested for the idea of faeces as territorial markers. In addition, some faeces were arranged in apparent "middens", frequently seen nearer the edges of the enclosure; this may have been the result of young cats using common areas near the "core" plus the spatial limitations of the enclosure.

A further consideration was the Rubbing of objects and its potential role as a means of Marking a home range. Cats were seen to Rub their cheek, lip and chin regions along prominent objects such as twigs, stumps and even shelters or the perimeter fence; the secretions of these facial regions are rich in fats and thought to have odours characteristic to the individual cats. The use of Rubbing on other cats is mainly discussed with other affiliative activities, while only objects are considered here. Adults were found to Rub more than Juveniles, and Males Rubbed more than Females, perhaps supporting the concept of Rub-Marks as territorial (or status) indicators. In one case, an Adult Female Rubbed a tree; moments later, the Adult Male sniffed the rubbed place and then Rubbed it himself. An interesting difference became apparent when Adult Males were compared; Zac Rubbed objects far more than did Trossachs, while Trossachs Sprayed significantly more than Zac. Several possible explanations can be advanced to cover this disparity: the results are due to individual variation and have no deeper meaning; the two Males had different degrees of territoriality and only Spraying fulfilled the role of a marker; or, the two forms of Marking have different characteristics and convey separate messages, which researchers have as yet to interpret. In regard to the last suggestion, object Rubbing may have received less attention from human observers because of the difficulty of distinguishing Rubs through odour or visual cues; however, Males were seen to perform different types of Marking on similar objects, for example on the walls of shelters containing Females and their kittens (Corbett 1979). Occasionally, cats were seen to Spray an object after Rubbing on it (Corbett 1979; Dards 1979; Panaman 1981), but never in the reverse order.

As for the idea of territoriality, relatively little firm support was found; Males did not appear to maintain their ranges through aggressive exclusion of others, and the pattern of Marks was not generally concentrated at the periphery of the ranges. What small evidence there was came from Trossachs' habit of pacing the dividing fence, from the occasional aggression between the two Adult Males, from the pattern of Male dispersion (Dards 1979; Liberg 1980; Kerby 1987), and from the arrangement of some "latrines" near the perimeter. Almost all of these observations can be explained by the

placement of groups in adjoining limited areas within full view of each other; Males may simply have acted as if an intruder were often present near the core area with the food source. Male dispersion probably has further functions and cannot be seen as mere competitive exclusion, as was discussed in the Introduction (Chapter 1). Reactions to an intruder were mainly observed when the truly feral cat (a Female) living near the study site investigated the study cats; this sparked strong agonistic displays both from the Adult Male and from Adult Females, and seemed more indicative of a potentially resource-guarding response. Inter-Male agonism may have resulted from the confining nature of the enclosure when the number of mature Males became large; Trossachs and his son, Pishi, demonstrated far less aggression than was seen in the other group (which had five Males instead of only two). In the light of Trossachs' tendency to Spray-Mark and patrol, perhaps he would have been expected to respond more agonistically to other Males in his group, although this was not the case.

Generally then, Females appeared to behave in a way that allowed the formation and maintenance of amicable relationships among themselves, while Males were more peripheral and seemed to have a looser connection with the group. Young Females matured into roles similar to those of their mothers and "aunts", and young Males remained outside the core except for associations with these mothers and "aunts" and among themselves. These young Males dispersed around the age of two years, and their lack of close social relationships with the rest of the group may have either predisposed such emigration or may have facilitated it. Kittens were quite active in terms of social interactions, and these were primarily initiated toward mothers and other familiar cats (especially Females), although the Adult Male was an additional subject for attention. One behaviour pattern seen during this study, but undescribed from other researches on domestic cats, was the activity termed "Rolling". It was not one of the specific Focal patterns, but was noted as an additional observation when it occurred. Rolling involved a cat rolling onto its back, often with legs splayed, and belly unprotected; much of the Rolling was seen to be initiated by Juvenile Males to Adult Males, and was strongly reminiscent of the submissive behaviour reported in canid societies (Fox 1975a; Poole 1985; Huntingford & Turner 1987). Some Rolling was also seen from Adult Females to Adult Males, but this was in the obvious context of mating, along with other oestrus-type behaviour, unlike that seen in young Males.

A new perspective was gained when the data were divided into component seasonal periods. Separation into months of the year was the initial step, as has been done in several other studies (Kerby 1987; Macdonald et al. 1987). Close spatial associations were found to clump into aggregations which echoed the general course of the reproductive

year and the weather, so that Winter clusters could be traced to cats who huddled together in shelters, presumably for heat retention, while spring and summer groupings mainly corresponded to breeding coalitions. At greater distances, increased levels of interaction were correlated with warmer and drier weather, suggesting that these associations were more random and were related to general activity throughout the enclosure and in the feeding areas rather than specific individual affiliations. The prevailing evidence supported weather effects on spatial associations and strongly hinted at some accompanying effect of reproductive state, so this was then examined.

Unfortunately, it proves particularly difficult to separate weather factors from reproductive ones, as increases in day length trigger the onset of oestrus, and are accompanied by general temperature rises and more sunshine. However, the details within the breeding year are less prone to such consistent weather effects after gestation begins, as spring and summer often share similar temperatures. Spatial relationships among reproductive seasons described a cyclical pattern, such that Winter and spring Gestation and Breeding were interconnected within and between years. The proposed mechanism explained this arrangement using both weather and reproductive factors. Close relationships, probably initially formed through early experience and familiarity (as seen in the Kittens and Juveniles), are reinforced throughout the Winter in the form of resting coalitions using common shelters (often cramming the huts to repletion); Gestation then follows from Winter, with some continuation of the cold weather and huddling, supplemented by mutual interest among pregnant Females. Birth synchrony allows Females to form cooperative groups, although it is not necessary (as seen in cases where pregnant Females "helped" mothers with litters and later pooled new kittens with them, despite large age gaps). The onset of cooler weather, along with the presence of mutually-reared young cats prompts a return to resting coalitions of similar composition to the previous year, although new members can be introduced (often following some cooperative effort). During second and third breeding attempts (in a single year), birth synchrony and cooperative groups seemed to break down, and were not part of the regular cycle of spatial associations, although it could be resumed in the Winter (after the uniform failure of later litters). Dyadic "preferences" for certain partners supported the concept that Females have relatively consistent types of relationships throughout the year.

After proposing this cyclic structure for groups of Female cats, the behavioural data were examined for any activities that might support and maintain affiliative associations. Once again, certain actions were correlated with weather changes, indicating that some activities might be more concerned with mating (e.g. Follow) and others with general affiliation (e.g. Groom and Rub). Monthly rates fell into subsets of activities, such that the early spring months (e.g. mating) involved a group of behavioural actions such as

Follow, Approach, Evade, Close Sniff and Rub. The way in which related actions (in terms of function) clustered and changed at similar rates with the times of year seemed to denote that reproductive states might have some role in behavioural variation. The seasonal behavioural trends were not as clear as with the spatial relationships, probably due to the more general nature of some activities. Over the entire year, breeding Females directed similar levels of Grooming, Swiping and Resting in Contact to other individuals, reflecting the constant presence of Males and other sources of conflict, the continued company of maturing offspring, and perhaps the relative stability of affiliations. In turn, Females received consistent rates of Approaches, Evades and Grooming from other cats.

With less specific actions, such as Follow and Approach, which could be part of several different behaviour categories (e.g. affiliative contact, agonism, mating), most seasons demonstrated related levels of interaction. However, with some of the more identifiably affiliative (and agonistic) activities, the same pattern was found as with spatial relationships; the rates of behaviour during the Winter and spring reproduction were interrelated and followed a cyclic pattern from year to year. Most behaviour initiated by breeding Females was consistent over Winter, Gestation and Breeding, and recurred both years, while having little association with later (second) reproductive efforts; this arrangement was particularly obvious when cooperative dyads were considered, for both communal partners and helpers. Perhaps Females seek out the same partners each year, based on past experience reinforced by stable relationships. Also, future cooperative coalitions were predicted by the behaviour seen in the preceding Winter as well as by the intensification of such associations during Gestation. Both affiliative and aggressive combinations were stable through the year, implying that relationships may take account of a variety of factors when forming and are then reinforced by continued interactions of a particular nature. Behaviour like Rubbing against other cats, although it is relatively rare and short in duration, may be sufficiently affiliative to hold social groups together (Macdonald et al. 1987), especially when supported by a range of other affiliative actions.

Therefore, both the spatial and behavioural data support the hypothetical structure wherein specific dyadic relationships, especially those of an affiliative disposition, are maintained at similar levels through the year, apparently facilitating the formation of cooperative coalitions during breeding. In order for this pattern to have any meaning or functional significance, some benefit to cooperation must be established.

The details surrounding reproduction were presented and briefly discussed in the previous chapter (Chapter 5), and will be examined here. The birth of litters was quite clumped in the spring months, March to May, with a second peak in June to August. All later-born litters had higher levels of mortality, including those from the first breeding

attempt. All second and third litters failed within six weeks of birth. Females used certain Nest Sites repeatedly and ignored other potential places; they also moved into the general area of the food source as kittens approached weaning age. The two groups of Females showed few differences in any reproductive variable, although Group A had proportionally more Primiparous mothers. When general effects of experience were investigated, using Primiparous and Multiparous Females, little variation was seen beyond the small Littersizes-at-Birth for Primiparas, as well as their significantly younger age than Multiparas. Primiparas were more often Communal, and may have spent slightly more time with kittens than their more experienced counterparts. However, in general, few differences were seen in the efforts of the mothers or the costs of kitten mortality as related to parity.

Communal care may well be facilitated or even triggered by birth synchrony, although this could not explain a number of cases where litters were pooled weeks after birth or where kittens of widely disparate age were combined. Communal litters were generally larger than Solitary ones, although there were exceptions. No difference could be found in the effort made by mothers of Solitary versus Communal litters, as measured by the proportion of time that they spent with the kittens. The one significant source of variation lay in the number of Nest Sites occupied by Solitary and Communal litters, in that Communal litters used twice as many nests over the first six weeks after parturition. The possible advantages of moving nest frequently were discussed at length in Chapter 5. Communal kittens also appeared to develop a little faster and left their nests much earlier than Solitary kittens; this might well have been due to increased strength or adventurousness on the part of Communal kittens, who moved Nest Sites more frequently. As with social behaviour, Females demonstrated a high level of individual difference in maternal variables, including the type of care shown and the number of kittens raised to independence. The large amount of within individual variation masked the differences between Females, so that other measures were not significantly discrepant among the cats.

"Reproductive success" was estimated as the number of an individual Female's offspring which survived to independence over all years of breeding (Kerby 1987); due to the complications induced by culling in 1988, the age used for this measure was four months, after which time little mortality was seen (and before which sporadic incidents of mortality were seen). Individual mothers had different totals by this calculation, and those who had large litters, but lost many kittens, were as "successful" as Females who had few kittens and low mortality rates. The most interesting aspect of the "reproductive success" estimate was shown when Communal and Solitary litters were compared: somewhat more Communal kittens survived, although the result was not statistically significant at the $\alpha = 0.05$ level. In other words, Females who were

cooperative in the sense of pooling litters raised more offspring, and potentially contributed more individuals to breed in the next generation. When all cooperation was considered, the joint attentions of mothers and other cats (helpers) resulted in significantly more surviving offspring than did the efforts of Solitary mothers alone (when Jenny was included in the analysis; this value became non-significant when she was excluded). Solitary kittens also had a higher overall mortality rate, even without the measure of "success", when all kittens were considered (including those that received no care). Unfortunately, the small sample sizes (e.g. number of mothers) and the occurrence of litter abandonment complicated the mortality measures, as discussed in Chapter 5 (Section 5.7). In summary, in this study, it would appear that cooperative rearing of kittens had some benefit in the form of enhanced kitten survival.

Cooperation took several forms in the cats participating in this study; in some cases, it involved two or more mothers pooling their litters, and this has been termed "communal" care in which both Females can "invest" in combined kittens. The second type was more "cooperative" and included mothers with kittens and non-breeding helpers or "aunts". Sometimes the cats involved were related (e.g. mother and daughter, or littermates), and at other times they were unrelated. Helpers included an old Female past her ability to reproduce, nulliparous Females (both Adult and Juvenile, kin and non-kin) and young Males (mainly mature offspring, but not confined to such individuals). Communal Females also showed two patterns; some mothers had striking disparities between the amount of time spent with the kittens, while others were more mutual in this measure of "effort". Despite several clear cases of unequal input of time, Females did not appear to strategically abandon kittens to their communal partners to reduce their own reproductive "investment".

For most of the shared litters, the relationships between cooperating cats seemed a key factor to the nature of the situation, and it is this element that the study aimed to elucidate. In many cases, the cooperating Females were also those individuals who shared affiliative relationships throughout the year; again it is proposed that the act of cooperating was an outcome of the social bonds maintained over time, and that cooperation bestows a significant advantage on the participants. Communal Females, who pool their litters, can both benefit from the situation, while it is harder to explain why helpers should exist. As discussed in both Chapter 1 and Chapter 5, cooperation may persist in the population through kin selection (e.g. advantages to relatives), through reciprocal altruism (e.g. future returned benefits) or through mutualism (e.g. immediately returned benefits), unless it is a trait carried by selection on related characters; any of these three mechanisms might be responsible for the cooperative rearing of offspring seen in cats.

One consideration was the common cooperation seen among unrelated Females, which suggests reciprocal altruism or mutualism as a selective mechanism. A complicating feature was produced by the conditions under which Females lived prior to the study; in fact, they were mainly kept together in a large facility, which either provided the grounds for the formation of relationships, or merely allowed the cats to become familiar with one another. In many species, it is suggested that familiarity is the cue for recognising kin (Bekoff 1981; Hinde 1983), in which case all Females in this study should act as if related; however, the subject Females did not interact equally with all others, and still formed "preferences" for certain behavioural interactants. Due to the blurred distinction between kin and "familiar" cats in the study, it is impossible to state why the founding Adults cooperated; however, the actions of offspring born into the colony gave additional insight into this question. Younger Females cooperated with their mothers and with their littermates, as well as with familiar Females; even young Males were seen helping with the litters of their mothers and familiar cats (Dards 1979). Proximate benefits to young nulliparous helpers might include learning experience (or the early induction of maternal behaviour) or the maintenance of social bonds which facilitate group-living (for both young Females and Males). Again, any of the three potential ultimate mechanisms could have supported such observations and maintained helping characteristics in individuals.

An anecdote which may help to elucidate the interaction between social relationships and breeding coalitions involved the Females Poppy and Tessa. This dyad had some underlying relationship prior to the 1989 breeding season, in that Tessa tended to Approach and Rub Poppy in an amicable manner, while Poppy initiated agonistic Swipes; Tessa was also seen to initiate Fights with Poppy without apparent cause. The relationship was not obviously stable nor amicable; then in 1989, Tessa gave birth to her litter in the nest that Poppy and her new kittens were using. Only two days after this, the combined litter (of eleven) was moved to a distant site, although neither Female was seen to visit or respond to the calls of kittens (audible to the observer). The kittens died shortly thereafter, apparently neglected and abandoned. The two Females continued to show high levels of agonism and avoidance throughout this period, and were aggressive even when they acted as co-helpers (and "sucklers") for a third litter born a few days later (a performance repeated again several months after this). The logical explanation was that one Female moved the litter away from the first nest, perhaps in response to the disruptive presence of her "partner"; Tessa might have acted in this way, as she was known to neglect previous litters, while Poppy was a consistently attentive and (until this occasion) "successful" mother. The second Female (probably Poppy) did not know the location of the new nest and was sidetracked by the arrival of new kittens in the first nest. The lack of response to distress calls is difficult to understand, but certainly occurred.

In the described situation, the lack of affiliative relations between communal partners appeared to lead to the mortality of the kittens through neglect; both Females may have avoided the combined litter in the face of renewed aggression while in the nest. The most likely reason for the pooling of litters was the presence of a third Female (Becky), a past affiliative and communal partner to both participants, in separate years. In fact, her kittens, born soon after the others, received care from all three Females, although Tessa was not as persistent and stopped attending after a few weeks. The anecdote serves as illustration of the necessity for a strong contact-based relationship to underlie cooperative efforts.

An additional consideration is the individual variability found in the behavioural characteristics of cats. As set out in the Introduction (Chapter 1), regardless of the source of individual differences (whether flexibility or developmental plasticity), the result is a marked variation in population characteristics partially dependent on the component member cats. If cooperation can be engendered in a population because of ecological benefits and differential effects on fitness, it may be found in those groups which have the conditions promoting it. Cooperation might become tied to other, heritable, behaviour traits such as a high rate of affiliative activity, and thus itself become genetically transferred, especially if individuals helped kin (Bateson & Turner 1988). If the tendency to act cooperatively is a heritable character, then it may arise in those populations with one cooperative founder as well as those with the necessary conditions for its initiation, thereby giving rise to the variation seen in previous cat studies.

In this study, individual differences were seen at a series of levels; cats showed variation in spatial relationships, in behavioural interactions and relationships, as well as in reproductive behaviour. Although only two major categories, Solitary and Communal, were extracted from the data, further variation was present: some mothers pooled their litters at birth while others pooled kittens some weeks later; in some pairs, both mothers were attentive to the kittens, while others showed a disparity between the females; some Solitary females were alone, while others had non-breeding helpers (as considered in Section 5.7). Multiple factors probably influence the differences seen, including birth synchrony, the nature of the relationship between the mothers (and helpers), and the individual characteristics of each female.

A further aspect of the reproduction seen in this study involves infanticide. Many kittens disappeared leaving only parts of their bodies as evidence of cannibalism; still more kittens left no trace, and might also be attributed to cannibalism. Despite observing two occasions when cats were consuming young kittens, there was no concrete proof of infanticide, and these kittens may have died of natural causes. However, circumstances

indicated that the kittens were alive immediately prior to being eaten, in that they had recently been seen in good health and immediate contemporaries were alive (in the case of neonates). Both observed acts of cannibalism were performed by Adult Females other than the mothers of the "victims". In one particularly strange incident, one Female was suckling her own older kitten while eating the small kitten of another Female; this second mother sat next to the "diner" during this episode, with little apparent response. Later the second mother abandoned her remaining kitten (the others were seemingly eaten) and helped with the first mother's (i.e. the "diner's") litter.

Primiparas occasionally ate some kittens, but these were likely stillborn anyway (due to the higher incidence of stillbirth in first litters). Males were rarely seen near young kittens, and were never observed to injure or eat neonates. Another interesting anecdote, which might act as an indicator of potential pressures, involved young Kittens and neonates. Kittens born three or four months earlier were seen with neonates (an unrelated second litter), playing roughly with the newborns and seeming to treat them like prey objects (e.g. tossing, batting and "worrying" the kittens). Blood was drawn, the neonates appeared battered and wounded, and they had disappeared (cannibalised?) by the following day. To compound the story, the mother of the neonates then acted as nursemaid to independent Kittens (several months old) and was suckled upon incessantly for many weeks by all the young cats of the group.

Based on these observations, infanticide might occur for several reasons in domestic cats, including as an outcome of late birth. It is possible that male cats are infanticidal as a means of stimulating females to return to oestrous cycling. This seems unlikely for several reasons: female cats apparently return to oestrous cycles quite rapidly compared to other species (Natoli 1990), so that infanticide may not speed the onset of oestrus; and the mating system whereby several males mate with the same female gives rise to the uncertainty of paternity (e.g. a male with access to a given female and her kittens could well be the sire of those kittens). However, infanticidal males could help to explain the defensive aggression of females with young offspring, and males in other studies have been observed to kill kittens (Macdonald et al. 1987).

Female cats might be infanticidal for various reasons: if unpredictable conditions become extremely limiting after parturition, infanticide and subsequent cannibalism may allow females to reduce their investment in the current litter while recycling some of the effort already made (Harper 1981; Wickler & Seibt 1983); or, in a society with high cooperation levels, females might kill the offspring of conspecifics to reduce their own communal input to others, while increasing that received by their kittens (Hoogland et al. 1989). The nutritional gains of cannibalism may also prompt infanticide (Gittleman 1985), although, in the present study, kittens were eaten when there was a surplus of available food. An additional consideration is contributed by the observation of

older kittens playing roughly with neonates; later litters born to a group, if pooled with much older kittens (e.g. three to four months old), may suffer from the attention of older companions. Once injured, neonates may resemble food more than conspecifics, especially in the absence of maternal inclinations.

Several of these scenarios suggest new potential costs to the tactic of cooperation in a population, such that it may increase the beneficial aspects of female infanticide. It is possible that choosing a particular communal partner may be additionally constrained by the chance of infanticide, which makes it all the more important to have an amicable and/or kin relationship with the partner prior to sharing. In the absence of an ability to discriminate one's own offspring in a communal nest, it might pay females to pool litters soon after birth, to inhibit potentially infanticidal encounters. Cooperation could just as easily arise as a way to reduce infanticide through increased guarding; the key is the identity of most infanticidal individuals. If familiar females perform more of the killing, then, cooperation might carry an attendant cost, whereas if males (or strange females) are the killers, then cooperation may well limit the possibility of intruders in the nest. The increased number of Nest Sites (and more frequent moves, as discussed in Chapter 5) observed in Communal litters may allow females to keep nest locations hidden. When found or disturbed, several females can move nest more quickly and efficiently, without risking unguarded kittens (a problem for single mothers, constrained to move kittens one at a time).

This thesis has set out to examine the cooperative relationships between individual cats, manifested as communal rearing of kittens and in the additional form of helpers. The main hypothesis was that, while food and other resources might impose limits on the formation and size of cat groups, the presence of sociality and affiliative relationships within such groups is due, at least in part, to the benefits conferred by cooperative reproduction. The main advantage to cooperative care in this study was the indication that the survival of kittens might be enhanced, compared to those litters raised by lone mothers. Females that cooperated contributed more offspring to subsequent generations. This measure was somewhat complicated by the problems of pooling samples and the occurrence of litter abandonment, but there remains some suggestion that cooperation could be sufficiently advantageous to shape behavioural traits. Cooperation could be maintained in the population through social relationships, which are reinforced throughout the year regardless of reproductive state. The structured and affiliative interactions seen in most studies of domestic cats (Macdonald & Apps 1978; Dards 1979; Liberg 1981; Panaman 1981; Kerby 1987; Macdonald et al. 1987) are proposed as an adaptive outcome of the pressures acting on cat (and especially kitten) survival, such that

they are required for the formation and consolidation of cooperative relationships between females.

Cooperative behaviour has been advanced as an explanation for the sociality seen in diverse species, but usually only concerns those coalitions for hunting, foraging and defence (Eaton 1979; Macdonald 1983; Gittleman 1989). The results of this study suggest that cooperative care of offspring may be as significant a force in shaping the sociality of those species that lack the circumstances for cooperative hunting. Further research is needed, linking aspects of reproduction with other behavioural characteristics; comparisons of solitary and communal strategies in free-living feral populations of cats would add some of the information missing from this study, which was constrained by its enclosed nature and by the artificial membership of groups (lacking the extensive matrilines seen in most other studies). The effects of relatedness, and the possible correlates of kinship which allow recognition of close relatives, would shed additional light onto the question of how cooperation is maintained in the population and which specific mechanisms are concerned. There was some indication that cooperative mothers have cooperative offspring, so that the trait may be heritable and characteristic of certain populations; it may also be that the social relationships formed with littermates and allomothers promote and facilitate later cooperation within affiliative dyads. The classification of infanticidal individuals, and more idea of the frequency of kitten-killing, would enable the identification of causes and effects of infanticide, and whether it is somehow linked with cooperation.

Cooperative rearing of young may reduce kitten mortality through various means, including increased transmission of antibodies in milk, optimisation of milk quality and quantity, increased guarding against predators and hostile conspecifics, the ability to move nests frequently and thereby maintain a cryptic location, or early socialisation into a feeding group (facilitating assimilation into the social group). It would enhance the understanding of cooperation as a possibly beneficial trait to know which of these (and other) elements play a role in individual populations. An important consideration is the fact that each population has a particular set of surrounding conditions, as well as specific member cats, so that completely different selective pressures may affect the social structure. Only by examining further free-living groups can we unravel some of the threads to look at group ecology in still more depth.

A young kitten, Camille, aged 15 weeks, and the neonates of Jenny. Camille has been playing roughly with these newborn kittens, and blood is clearly visible on the back of the one on the right. These kittens were not seen to be suckled by the mother (or any other female) and disappeared overnight. (see Chapter 6)

Two adult females, Tessa (hissing, on the right) and Poppy, surrounded by kittens. Both females are pregnant with second litters. (see Sections 4.3.1, 5.5.5, and Chapter 6).

Chapter 7

Summary and Conclusions

7.1. GENERAL SUMMARY

Female cats tended to aggregate together, often near the feeding area or "core", along with many of the Juveniles and Kittens when present. Males were mainly seen at some distance from other cats, and only occasionally were they found close to Females and other individuals. Juveniles often formed a separate cluster within the group, and associated together and with Kittens. Females who cooperated at some time during the study had particularly high levels of close interaction. Some Females were found more with their own Kittens than with those of other mothers, while other Females seemed to prefer the company of unrelated Kittens.

There was some indication that proximity relationships included Central and Peripheral individuals, as well as those occupying more intermediate positions of the continuum. Proximities less than thirty centimetres appeared to be the most sensitive to social relationships, while distances greater than one metre were reflective of more general associations.

More social behaviour was exchanged between Adult Females than between any other combination of cats, and these activities were mainly amicable. Male-Female encounters were primarily concerned with mating, although Females did initiate affiliative behaviour toward Males. Males showed predominantly investigative types of behaviour to Juveniles, with additional agonism to young Males and reproductive actions to young Females. Juveniles interacted most amicably with their littermates and familiar Females. Kittens typically received amicable and maternal behaviour, and were initiators of some social interactions. Overall, the rates of behaviour initiated by any individual were related to the levels received.

The cats showed a large amount of individual variation in all proximity and behavioural measures, and these probably influenced dyadic relationships. Some pairs of Adults demonstrated significant asymmetries in the rates of initiated social behaviour , while other dyads were more balanced or mutual in the direction of actions. All cats had more common, or preferred, partners for different proximities and different behavioural interactions. Females varied in the proportion of Nursing they did with their own versus other Kittens; some Females Nursed unrelated Kittens more than their own, although this was not common.

All Males were seen to make Mount attempts, but not all of the individual Males copulated successfully. The founding Adult Male of each group performed most of the copulations with Adult Females.

Affiliative, or contact, behaviour was the most common form of social interaction, followed by vocalisations. Agonism, especially in any escalated form, was fairly rare.

Females were seldom observed to Spray-Mark, although Males did so frequently. The pattern of tree-scratching followed common pathways through the enclosure, and did not concentrate along any "territory" boundary. It is likely that one of the factors affecting Scratching was the type of tree, as cats favoured species with softer bark. Object Rubbing was also treated as a form of Scent-Marking; Adults Rubbed more than Juveniles, and Males Rubbed more than Females. Individuals again showed differences in these activities. Cats tended to eliminate away from the feeding area (e.g. more than 10 metres); faeces were often left exposed, but no clear pattern was discernible.

A form of Rolling behaviour was observed, in that young Males often Rolled to Adult Males, displaying their bellies. Females also Rolled to Males, but this appeared to be in the context of mating solicitation.

Spatial relationships described a cyclic arrangement when separate reproductive seasons were considered. Winter and spring Gestation and Breeding relationships were related within and between years, while second and third reproductive attempts had dissimilar spatial associations. It would be possible to predict spatial relationships from one year to the next, based upon the reproductive state of Females.

Social relationships based on behavioural interactions also showed a cycle when reproductive seasons were distinguished, with Winter again interrelated with spring Gestation and Breeding, within and between years. This was especially true for more affiliative activities and for cooperating individuals. Other, more general, behaviour patterns were consistent through the year, probably due to their unspecific nature (and involvement in different types of encounter). Social behaviour showed evidence of seasonal and yearly stability.

Females showed a degree of reproductive synchrony, and most litters were born in March to May. Second litters were often born within a single year, but all of these

later kittens failed to survive. Some Females had no litters throughout the three years of the study, despite being mated.

Very few differences were seen between Primiparous and Multiparous mothers, in terms of litter survival or maternal effort, as measured by the proportion of time Females spent with their litters. Primiparas tended to be young and usually gave birth to only one or two kittens.

Litters raised through Communal and Solitary care showed few differences in maternal effort, measured as Time Budget, and Kitten Mortality. However, Communal litters used twice as many Nest Sites as Solitary ones, and Communal kittens typically left the nest (for the first time) a full week before Solitary kittens.

A slightly larger number of Communally-reared kittens survived to four months than did Solitary kittens. However, significantly more kittens from cooperative litters (Communal plus those with helpers) survived than those reared by Solitary mothers alone. Survival to four months was used as a rough estimator of Female "reproductive success", along with the number of breeding years. From this measure, there would appear to be some indication of a benefit to being Communal or cooperative (for the mother), in the form of enhanced offspring survival.

Cannibalism was observed during the study, and infanticide was suspected from the circumstances surrounding the cannibalism. As many as 29% of all kittens born may have suffered cannibalism, although the known cases accounted for only 7%. Infanticide may or may not have preceded the consumption of kittens, but probably was not the cause of death in all cases. Adult Females were the cats observed performing cannibalism, and both these individuals were lactating at the time, although they were not the mothers (or allomothers) of the "victims".

General nest location changed through the first six weeks after birth, such that later nests, containing kittens approaching weaning age, tended to be nearer the food source. Different females used the same locations, sometimes repeatedly for the same litter. Some sites were used only rarely or not at all, suggesting a choice of specific locations; factors may include the degree of shelter, the placement of food sources, and perhaps the proximity of other females and nests.

7.2. CONCLUSIONS

This study has examined the nature of social relationships in domestic cats, with the aim of elucidating the frame upon which sociality is based. Cats are known to be solitary foragers and hunters, and as a result, the formation of social groups, with strong affiliative relationships, has been largely unexplained. Some authors have a tendency to dismiss domestic cat sociality as a construct ensuing from the process of domestication. Much of the argument relies on the observation of related species, such as *Felis silvestris*, the European wildcat, and their solitary habits; however, it would appear that the wildcat (among others) has some ability to form affiliative relationships and even cooperates in the rearing of young when presented with conditions which allow and promote this. The evidence indicates that domestication is not the only explanation for domestic cat sociality; perhaps now the domestic cat can take its place next to the other documented social felid, the lion, and can contribute further insight towards explaining the formation and maintenance of groups in carnivores.

The cats studied here had a structured social organisation, both spatially and behaviourally; the affiliative relationships usually corresponded to cooperative dyads in the breeding season. It is postulated that the reinforcement of affiliative relationships occurs throughout the year, regardless of reproductive states, and acts as the basis for partnerships when kittens are born. Kittens reared by more than one mother or with helpers had a higher survival rate than kittens with lone mothers, suggesting a clear benefit both to cooperation and to the maintenance of any relationships which might facilitate cooperation.

Therefore, the main conclusion of this thesis is that, where resources allow the formation of cat groups, sociality exists as the basis for the formation of amicable relationships, which in turn may act as the foundation for cooperation. Through cooperation, females can enhance the prospects of survival in their kittens, and thereby potentially contribute more offspring to subsequent generations.

Young kittens in a nest, attended by two older males. Duffy, a one-year-old, is seated, and is unrelated to the kittens. The other is Catkin, a two-year-old by the same mother (Calico). (see Section 5.5.5)

Calico and one of her kittens, in a nest inside a wooden hut. The mother is hissing at the proximity of an intruder.

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APPENDIX A: Samples of the Checksheets Used in this Study

SPACING OF INDIVIDUALS

DATE	TIME	NAME	POSITION	ACTIVITY	IN CONTACT	≤ 6 INCHES	6" < d ≤ 1 ft	1ft < d ≤ 1m	1m < d ≤ 5m	"IN SIGHT"	"OUT OF SIGHT" (OOS)
		TROS									
		KAT									
		BEC									
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		PAN									
		POP									
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		CAL									
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		ZAC									
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		LAU									
		MOL									
		DAI									

FOCAL - ANIMAL WATCH

SOCIAL INTERACTIONS

FOCAL ANIMAL:

DATE:

WEATHER:

TOWER OR ENCLOSURE:

TIME	LOCATION	ACTIVITY (RATE SEQUENTIALLY/INDIVIDUALS INVOLVED)																						NOTES (INCL, RESPONSE OF INTERACTING INDIVIDUALS)
		FOLL	APPR	EVADE	N°	CONTACT						AGONISM						MATING		PLAY		SCR	MARK	NURSING		GR	VOCALISING	
						R/C	SL/C	CH/HD R/B	H/RUB	CS/NA	PAW	SW	EFLAT	PILO	FLASH	BIT	FGH	♂ M/T	COP	♀ DISP	O/PY	S/PY			OWN	ALLO		M, Y, C, BR, HS, P, GW, PR	
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CONTINUOUS RECORDING

ENCLOSURE SIDE:

DATE:

START TIME:

STOP TIME:

WEATHER:

TIME	INDIVIDUAL	POSITION	ACTIVITY DESCRIPTION	NOTES

TIME-BUDGETING BY MOTHER

NAME OF MOTHER:

DATE:

LOCATION OF KITTENS:

DATE OF BIRTH:

PAGE OF PAGES

TIME	MOTHER			OTHER CATS ≤ 1 m OF KITTENS		OTHER OBSERVATIONS (e.g. weather)
	✓ WITH KITTENS	LOCATION	ACTIVITY	NAME	ACTIVITY	

APPENDIX B: Behavioural Definitions Which Were Supplementary to Those Used in the Analysis of Relationships

Feed: Cat is either drinking water (from a dish or other source) or eating (from the provisioned food or prey sources).

Hunt: **Rove**: Cat is generally making a searching perambulation, which includes stationary alertness.

Stalk: A locomotory action in which paws and legs are lifted high, the body is kept close to the ground, with head down and eyes fixed on prey.

Chase: Cat follows prey closely, usually at high speed.

Spring: Cat jumps from crouched position at prey.

Paw: Cat bats at prey with a single paw, often called "Cuff".

Hold: Cat grasps prey in both paws.

Bite: Cat nips at prey, often directing toward the nape of the neck.

Eat: Cat consumes prey.

There are further prey-related actions, often with insect subjects, which were not elucidated (after Panaman,1981; Tan and Counsilman,1985).

Locomotion: Walk: Cat moves upright at a regular, unhurried pace.

Walk Alert: Cat walks, occasionally stopping to look around watchfully.

Crawl: Cat moves with body in a crouch position, with body lowered to the ground, forepaws tucked under the body and forelegs flexed. Often appears watchful or wary.

Dart: A rapid movement over a short distance, often proceeding from walking or another locomotor form.

Run: A rapid locomotion over longer distances.

Bound: Cat uses a springing method of running, frequently leaping quite high with each "bound", often through long grass. Propulsion is mainly by the hind legs.

Pick: Cat moves quite slowly, lifting legs fairly high and in a deliberate manner, as if watching each step.

Patrol: An action performed mainly by Trossachs, in which a cat moves along "set" paths, often at the perimeter of the enclosure, in a deliberate and searching manner. This movement can be quite rapid, although not at "run" pace, and may involve the retracing of the cat's own steps.

Pace: Cat walks back and forth over the same approximate area, path or entire route more than once.

Explore: Cat walks while sniffing or with nose lowered to the ground. This is often slower than a walk and may include some pauses.

Rest: Cat lies, sits or stands while awake, but without body movement, and eyes are often shut (after Panaman,1981).

Sleep: Cat lies with head resting on its own body, the ground or the body of another animal, eyes closed and body relaxed (after Panaman,1981).

Urinate/Defaecate: Self-explanatory actions, which often include clawing at the substrate (grass or ground) before and/or after deposition.